Environmental and Genetic Factors Affecting the Physiology and Ecology of Lake Trout

Lake Trout Synthesis
Physiology and Ecology Working Group
1990

Ontario
Ministry of
Natural
Resources

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ABSTRACT

MacLean, N.G., J.M. Gunn, F.J. Hicks, P.E. Ihssen, M. Malhiot, T.E. Mosindy, and W. Wilson. 1990. Environmental and genetic factors affecting the physiology and ecology of lake trout. Lake Trout Synthesis, Ont. Min. Nat. Resour. Toronto. 84p.

The role of genetics, feeding ecology, habitat and spawning behaviour in the management of lake trout (*Salvelinus namaycush* is examined. Evidence for genetic differences and environmental effects among both native and hatchery stocks of lake trout are discussed. To maintain healthy lake trout stocks and to rehabilitate degraded stocks, genetic principles aimed at preserving genetic variation, minimizing artificial selection and maintaining stock structure need to be adopted. The implications of adopting these principles to lake trout harvest control, culture and stocking are discussed. A review of lake trout feeding ecology indicated that lake trout at all life stages are omnivorous, opportunistic feeders and that it is the quantity, quality and availability of prey type together with fishing mortality that determines the potential growth patterns of a stock and account for the observed size composition of the population. Managers have tried to enhance lake trout growth by the introduction of prey species. Intentional and unintentional introductions of ciscoes, mysids, alewife, and smelt have been unpredictable and often destructive to native lake trout and other aquatic organisms. A lake trout habitat model based on a volumetric measure of temperature and oxygen is examined in light of physiological and spatial distribution data. The association between these habitat volumes and lake trout reproductive status is investigated. Minimum habitat volumes are recommended to protect self-sustaining lake trout populations. Multiple regression analyses determined that angling effort and that volume of a lake with an upper temperature limit of 15.5^{o}C and a lower oxygen limit of 4 mg L^{-1} were the best predictors of lake trout annual harvest. Managers can equate a loss in habitat with a potential reduction in lake trout harvest. Lake trout spawning behaviour and the characteristics of lake trout spawning shoals are reviewed. A simple key to identify the likely location of lake trout spawning shoals is developed for small inland lakes. Finally, management strategies related to lake trout genetics, feeding ecology, habitat, and spawning behaviour are presented.

INTRODUCTION

This paper examines the genetics, feeding behaviour and diet, habitat, and spawning behaviour of lake trout (*Salvelinus namaycush*) and discusses the role of these factors in the management of lake trout.

Fish species in general and salmonids in particular, are composed of genetically differentiated subpopulations, called stocks, which have the highest fitness in their native habitats. Genetic aspects of fish stocks have been explored in several recent symposia (Soule 1980; Billingsley 1981; Ryman 1981). These symposia have alerted biologists and managers to the potential for genetic erosion of wild fish stocks by human activities. Transplantation and matched planting experiments have demonstrated that fish stocks, including lake trout, can have very different fitness in terms of growth, survival and natural reproduction in different habitats. We discuss the role of the environment in determining phenotypic expression and review the evidence for genetic differences and environmental effects among both native and hatchery stocks of lake trout. Then, we discuss the implications of adopting genetic principles to the management of lake trout.

Lake trout diet and feeding behaviour varies widely with life stage and forage base diversity. Yet, many managers are concerned that specific food requirements may exist for healthy lake trout populations and wonder if prey manipulations would be a useful management tool. To assess the validity of these concerns, we reviewed the literature on the diet of various lake trout life stages, with particular attention to the effects of planned or unintentional introductions.

Currently, lake trout habitat models are being developed by the Ontario Ministries of the Environment (OMOE) and Natural Resources (OMNR) to predict the effects of nutrient input from shoreline development on the oxygen and temperature regimes of lake trout waters (OMOE and OMNR 1986; OMOE 1987). Such models are a potentially invaluable tool for plan review. We examined the lake trout's spatial distribution patterns and physiology to better define lake trout habitat in terms of temperature and oxygen, and then evaluated the habitat constructs currently used in these models. The relationship between lake trout habitat, reproductive status and annual sport fishing harvest was also investigated.

Locating and protecting lake trout spawning habitat is a prime concern of managers when assessing the impacts of shoreline development, or water level fluctuations. We reviewed lake trout spawning behaviour and on a more practical level, developed a simple key to identify the likely location of lake trout spawning sites in small inland lakes.

Management strategies related to the physiology and ecology of lake trout are presented.

GENETICS AND LAKE TROUT MANAGEMENT

PHENOTYPIC AND GENOTYPIC VARIATION AMONG LAKE TROUT POPULATIONS: THE ROLE OF THE ENVIRONMENT

Commercial fishermen on the Great Lakes were probably the first to recognize local differences among lake trout populations (Brown et al. 1981; Goodier 1981). Lake Superior fishermen traditionally distinguished at least four main forms (leans, humpers, half-breeds and siscowets) on the basis of spawning time and location, body weight and form, flesh and skin colouration and non-spawning distribution.

The idea that these phenotypic differences result, at least in part, from genetic adaptations that better equip a particular population for survival under local conditions is the central component of the stock concept. However, phenotypic differences do not always reflect genotypic differences. Phenotypic differences between local populations can result from genetic effects, environmental effects, or from an interaction of genetic and environmental effects. A common problem for fisheries managers is to determine whether a phenotypic difference is caused by environmental or genetic effects, or both. For example, if lake trout grow faster, mature earlier and sustain higher yields in one lake compared to another, how much of this difference is due to environmental effects or to genetic differences between the stocks in the two lakes, and how much is due to the combined effects of both genetics and the environment? If hatchery lake trout are planted on top of a remnant, endemic population and only the native fish continue to reproduce with no apparent genetic contribution from the planted fish, is this the result of the environmental or the genetic history of the planted fish?

EVIDENCE FOR GENETIC DIFFERENCES AND ENVIRONMENTAL EFFECTS AMONG FISH STOCKS

A wide variety of behavioral, physiological, morphological and biochemical characters in fishes are genetically determined (Ihssen et al. 1981). However, few studies have been carried out on the lake trout. Thus, research is needed to identify genetically controlled characters that can be used to distinguish among lake trout stocks.

In general, physiological and behavioural characters exhibit extreme "environmental plasticity". That is, the environment can alter the degree to which a particular variable is genetically controlled. For example, Rupp and Redmond (1966) observed that while stream spawning rainbow smelt, *Osmerus mordax*, became shoal spawners after transplantation to a lake, another stock retained its habit of late season spawning, even after transplantation to a lake in which previous smelt populations had spawned earlier.

However, experiments in controlled environments have suggested that many physiological and a few behavioural differences among stocks do have a genetic basis. Several studies have demonstrated genetic differences among lake trout stocks: hatching and emergence times and heterochrony (the acceleration or retardation of one developmental process relative to another) (Horns 1985); growth rate (Haskell 1952); swimbladder gas retention (Ihssen and Tait 1974); and age of maturity and spawning time (P.Ihssen, OMNR, unpubl. data).

Nevertheless, these investigations illustrate a fundamental dilemma- many physiological and behavioral differences can only be measured by comparing stocks in the same environment-whereas the manager is primarily interested in the adaptation of different stocks to different environments. To effectively

apply the stock concept to lake trout management, future investigations must concentrate on both ecological studies comparing different stocks in different environments, as well as matched plant experiments comparing different stocks in the same environment and the same stock in different environments.

Biochemical characters apparently are entirely genetically determined. No environmental effects were recognized in studies of lake trout by Stegeman and Goldberg (1972); Yamauchi and Goldberg (1973); May et al. (1979; 1980); Clayton and Ihssen (1980); Dehring et al. (1981); and Ihssen et al. (1988). In the course of these biochemical studies, polymorphisms (the occurrence of different genes at the same chromosone locus among individuals) for enzymes, proteins and eye pigments were discovered. Stocks differ in the frequency of these polymorphisms and sometimes for the presence of genes associated with these polymorphisms. In general, lake trout originating from the same refugia of the last glaciation are genetically more similar than those originating from different refugia (Ihssen et al. 1988). Sympatric stocks (those which occupy the same or adjacent territory) also tend to be genetically more alike than allopatric stocks, which do not occur together. Lake trout stocks from large lakes tend to have more genetic variability in terms of the number of polymorphic loci than stocks from small lakes. Using enzyme polymorphisms as markers, Ihssen et al. (1988) demonstrated that sympatric lake trout stocks in large lakes (Lake Superior) do not freely interbreed but are differentiated into reproductively isolated subunits. Recently, chromosome morphology and banding has also been used for stock differentiation (Phillips and Ihssen 1984, 1985, 1986, 1989; Phillips et al. 1989).

Crossbreeding experiments under controlled environmental conditions have shown that the environmental history of the female parent may also play an important role in adaptation. Differences in early stages of development (Ayles and Berst 1973) and vertebral numbers among lake trout (Dentry and Lindsey 1978) have been attributed to these "maternal effects".

EVIDENCE FOR GENETIC DIFFERENCES AND ENVIRONMENTAL EFFECTS AMONG HATCHERY STOCKS

Comparisons between hatchery and wild stocks in similar environments have demonstrated numerous behavioural, physiological and developmental differences that are believed to result from unintended genetic adaptation to the artificial conditions in the hatchery over successive generations (Flick and Webster 1976; Fraser 1981; Allendorf and Ryman 1987). Transplanted lake trout stocks often do not perform as well in terms of survival and reproduction as native stocks (Plosila 1977; Krueger et al. 1986). Brown et al. (1981) discussed possible effects of hatchery rearing on lake trout, which may be responsible for lack of natural reproduction in the wild. However, reproductive problems are not specific to hatchery lake trout. Most adult salmonids originating from hatchery yearlings are inferior spawners compared to wild fish (Kincaid 1983; Fleming and Gross 1989).

Electrophoretic techniques have also been used to show distinct genetic differences between wild and domesticated stocks. Several studies have documented a loss of genetic diversity and genetic drift in domestic as well as transplanted stocks (Allendorf and Utter 1979; Allendorf and Phelps 1980; Ryman and Stahl 1981; Ihssen et al. 1988). This loss in genetic variability has been associated with loss in fitness in a variety of animals including

fishes (Allendorf and Leary 1986). For example, Altikhov and Salmankova (1987) observed that as the genetic make-up of transplanted Pacific salmon (*Onchorhynchus* spp.) became increasingly dissimilar from their parent stocks, return rates decreased. Ryman and Stahl (1981) attributed the loss of genetic variability and genetic drift in hatchery stocks of brown trout (*Salmo trutta* to the use of too few founding parents.

When hatchery stocks are planted in lakes where native stocks are present, they can genetically impact native stock structure via introgression (the invasion of the genes of one species or stock into the gene pool of another). Introgression is believed to cause the break-up of adaptive gene complexes in addition to the loss of genetic variability, if the introduced stock has reduced variability. The mechanism that has been proposed is that an environmental disturbance may provide initial conditions favouring the non-native stock. First generation hybrids can also have a fitness advantage and out-compete the native stock. In subsequent generations, as the local and introduced genes segregate and hybrid vigour declines, a less fit stock results. Continuous planting can eventually completely replace the native gene pool with the donor gene pool. The donor stock does not need to be as well adapted to local conditions because it goes through part of its life cycle under sheltered hatchery conditions. The lower fitness of the introduced stock only becomes evident after stocking is discontinued and the introduced stock is obligated to spend its complete life cycle in the wild.

Although only circumstantial evidence of introgression exists for lake trout (Ihssen et al. 1988), this phenomena has been documented for rainbow trout (*O.*

mykis) (Allendorf et al. 1980); brown trout, (Ryman 1981); and minnows (Hubbs 1955).

Differences in performance due to environmental effects are thus evident which are difficult to distinguish from genetic effects. In hatcheries, higher temperatures than those experienced in the wild are often employed for incubation. Such temperatures can permanently displace morphological (meristics, Hallam 1974; Murray and Beacham 1989) and physiological (respiratory physiology, Balon 1980a,b) characters from those in naturally produced fish. As temperatures approach $10^{o}C$, lake trout embryos have increased mortality and higher incidence of deformities (Ayles and Berst 1973; Christie 1981). Reduction of oxygen levels also affects larval lake trout, slowing development and increasing mortality. For example, few larvae survive at 4.5 mg L^{-1} O_2 (Garside 1959; Carlson and Siefert 1974; Balon 1980a,b).

MANAGEMENT IMPLICATIONS

The extensive genetic differences among fish stocks occur as a result of adaptations of populations to local environments. Case histories prepared for the SCOL symposium (Loftus and Regier 1972) documented the widespread environmental degradation and exploitation of salmonid communities that have resulted from human activities. It is clear that to maintain healthy (fit) lake trout stocks and to rehabilitate degraded stocks, fisheries managers need to adopt genetic principles aimed at preserving genetic variation, minimizing artificial selection and maintaining genetic stock structure. The management activities related to these principles include: harvest control, fish culture, and stocking.

Harvest Control

Selectively harvesting different phenotypes within a stock may genetically alter a stock (Ricker 1981). However, the artificial selection pressures associated with selective harvesting are not well understood. A better understanding of phenotypic variation of characters selectively harvested is required before the full impacts of various quotas, size limits and slot limits can be assessed. One of the main concerns of multiple stock fisheries is the possible elimination of some stocks. As the more productive and desirable stocks are usually more heavily exploited, fisheries managers must know if such stocks are genetically unique. Also, Evans et al. (1990) suggested that differential exploitation rates between native and planted lake trout can lead to loss of native stocks.

Fish Culture

To prevent the loss of genetic variability, it is imperative that fish culturists follow established guidelines for founding and maintaining hatchery brood stocks of lake trout (Hynes et al. 1981; Ryman and Utter 1986). It is preferable not to maintain a brood stock, but rather to collect reproductive products annually over the entire duration of a spawning run.

Research to identify and reduce detrimental genetic and environmental effects of artificial hatchery environments is also required. For lake trout, it has been suggested that hatchery environmental conditions (primarily temperature and oxygen) be closely matched to that encountered by healthy wild populations (Ihssen 1984). Higher temperatures and reduced oxygen can affect the physiology and morphology of lake trout embryos and may result in fry being out-of-phase with normal environmental cycles after stocking (e.g. increased

development may put emerging lake trout fry out-of-phase with a spring algal bloom). "Maternal effects" may also necessitate that hatchery managers more carefully control the environmental history of adult female lake trout.

The poor reproductive success associated with stocking yearling lake trout on spawning shoals (Brown et al. 1981), suggests that early life history plantings of eggs and/or fry need to be evaluated. Stocking early life stages would avoid many detrimental genetic and environmental effects acquired in the hatchery environment. If successful, such methods could be more cost effective.

Stocking

Although habitat protection/rehabilitation should always be considered as a first option, once a manager has chosen to stock lake trout, the primary concern should be to select a donor stock with high fitness in the receiving environment. The choice of stock should be in the following descending order of priority: same shoal; same lake; a sanctuary stock from a previously established genetic "refugium"; same watershed from a biotically and abiotically similar community; and a hatchery stock originating from a habitat which closely matches receiving waters. The preferred option for the donor stock will depend on the purpose of stocking and local conditions.

Several interesting observations concerning stocking success have emerged from recent biochemical studies (Ihssen et al. 1988). Discrete, sympatric lake trout stocks appear to be a large lake phenomena, probably only occurring in waters over 300,000 ha. There is circumstantial evidence that lake trout

stocks from larger lakes, with greater genetic variability are capable of colonizing a wider range of habitats.

Supplemental Stocking - Supplemental stocking is used throughout Ontario to increase available fish and fishing opportunities. Supplemental stocking can have a negative impact on wild stocks through: predation of planted yearlings on younger naturally reproduced lake trout; competition between hatchery and naturally reproduced yearlings; introgression (if genetically inferior planted fish interbreed with native fish, native stock may be displaced); physical displacement of native fish from spawning sites (Evans et al. 1990); and socioeconomic factors (planting fish may change the expectations and behaviour of the clientele, inadvertently increasing exploitation rates on native stock).

Supplemental stocking of naturally reproducing lake trout lakes should be discontinued. Managers should use habitat and community rehabilitation as a means to increase lake trout harvests and fishing opportunities. Moreover, client groups should be educated to develop realistic expectations about the resource.

Rehabilitation - The purpose of rehabilitative fish stocking is to restore balanced, naturally reproducing fish populations. Careful examination of a particular fishery is always required before rehabilitative stocking is undertaken to determine the real reason for the deterioration of fish stocks. Rehabilitation may be achieved by means of habitat rehabilitation and harvest control alone. In any event, these two management strategies should be implemented in concert with any stocking program. Although a manager's

objective in using hatchery fish for rehabilitation purposes may differ from supplemental stocking, the genetic consequences are probably identical. As such, managers should always consider other management actions as a first option.

Lakes which have lost their native lake trout populations should be rehabilitated if suitable lake trout habitat still exists. By continuing to manage these fisheries for lake trout, the manager will not only divert angling pressure from native lake trout stocks in other lakes, but ensure the high quality environmental protection afforded lake trout waters by current legislation. Sanctuary stocks or stocks from a nearby lake with similar biotic and abiotic characteristics would be the first choice as donors. If such donor stocks are not available, matched plantings of genetically diverse stock should be considered to determine the most appropriate stock.

Introductions - Some success has been achieved at establishing naturally reproducing lake trout populations in barren inland lakes (Olver and Lewis 1977; Purych 1980; Hitchins and Samis 1986). Limited success has also been achieved in some areas of the Great Lakes (Nester and Poe 1984; Peck 1986). However, in Ontario, before lake trout are introduced to a lake which has never contained lake trout previously, an environmental assessment is required to evaluate any possible negative impacts on the existing fish community. If environmental conditions permit, and no negative impacts on the existing fish community are foreseen, stocking lake trout is an appropriate management option, especially if a self-sustaining population is anticipated.

LAKE TROUT FEEDING ECOLOGY

The frequency of occurrence of major food items in the diet of lake trout alevins, young-of-the-year (YOY), juveniles and adults is shown in Fig. 1. Although this figure probably accurately depicts the relative importance of various food items in the diet of early life stages, it is less precise for latter life stages due to seasonal variability and community diversity.

ALEVINS AND YOUNG-OF-THE-YEAR

There is very little information on the food habits of young lake trout, especially alevins (30-50 mm total length (TL)) and larger YOY. Lake trout begin to actively feed at 25-27 mm in length, even before the yolk sac is fully absorbed (Balon 1980a; Swedburg and Peck 1984). Gunn and Kellar (1981, 1984) observed that emergent alevins fed heavily on planktonic crustaceans, especially ostracods, copepods and cladocerans, while the aquatic larvae of insects (ephemeropteran and hemipteran larvae, dipteran pupae) were of secondary importance .

Crustaceans remain the primary food of young trout after they migrate to deeper waters. Eschmeyer (1956) and Van Vliet and Qadri (1970) reported that *Mysis relicta* and the deepwater amphipods, *Pontoporeia hoyi* and *P. affinis* were major food items of alevins. In contrast, chironomids, especially pupae, were the dominant food items of emergent alevins during spring and early summer in the shallow nearshore waters of Presque Isle Harbour, Lake Superior (Swedburg and Peck 1984). Copepods, cladocerans and mysids were also present in the diet, but were of minor importance. Alevins in tributary streams entering a Connecticut lake (Kendall and Goldsborough 1909) and at Pyramid Lake, Nevada (Neave and Bajkov 1929) fed on adult terrestrial insects in

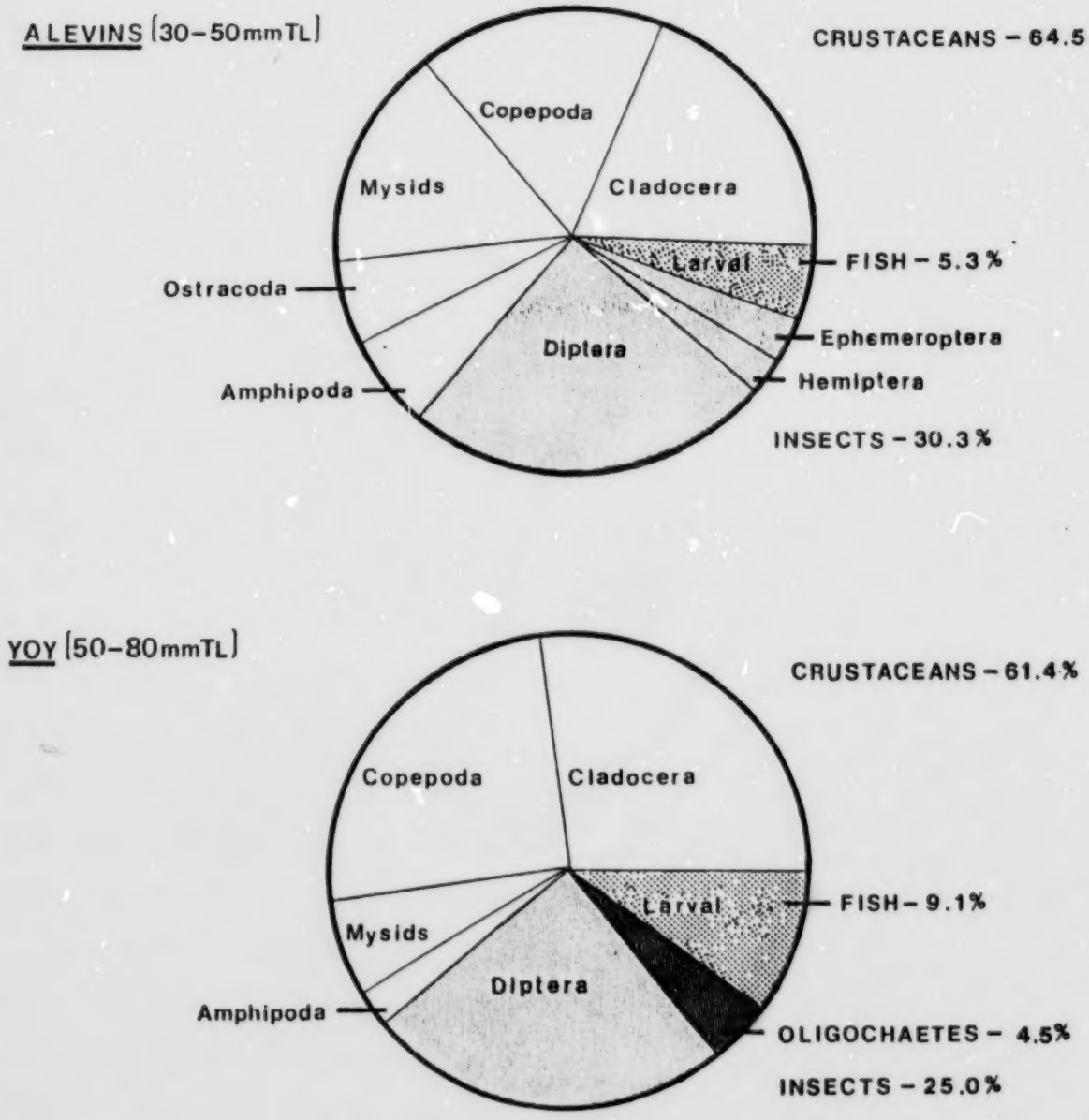


Fig. 1. The frequency of occurrence of major food items in the diet of lake trout alevins, young-of-the-year (YOY), juveniles and adults.

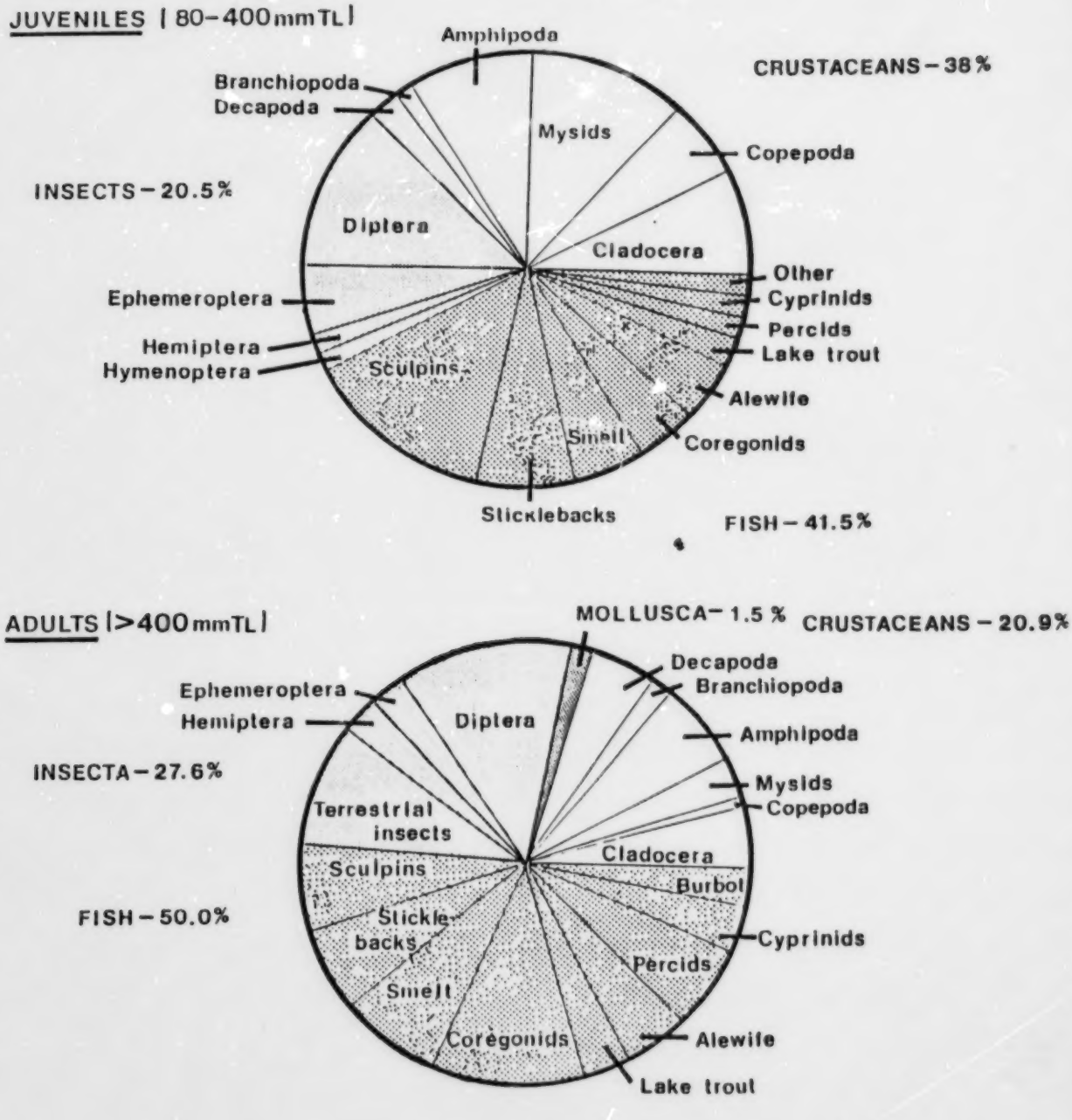


Fig. 1 . (continued)

addition to chironomids. Fish larvae (*Cottus* spp. and rainbow smelt) have been observed in the stomachs of 31 - 48 mm TL alevins from Lake Superior (Eschmeyer 1956; Swedburg and Peck 1984).

Young-of-the-year lake trout (>50 mm TL) also rely on invertebrates in their diet throughout their first year of life. Cladocerans and, to a lesser extent, copepods and amphipods formed the primary food of young lake trout in the deeper waters of Lake Tahoe, California (Franz and Cordone 1970) and Thompson Lake, Maine (DeRoche 1969). YOY lake trout which inhabited the shallower waters of Presque Isle Harbour, Lake Superior during late spring-early summer fed extensively on insect larvae, especially Chironomidae pupae (Swedburg and Peck 1984). Secondary items in the diet included mysids, cladocerans, copepods, and fish larvae (i.e. sculpins and rainbow smelt). The occurrence of larval fish in the diet increased as summer progressed.

JUVENILES

Most studies have found that the diet of young lake trout gradually changes, as the size of trout increases, to progressively larger food items; especially fish when available (Martin and Olver 1980). Smaller juveniles still rely heavily on invertebrates, primarily crustacean zooplankton and the aquatic larvae of insects, during the first few years of life (Fig. 1). Dryer et al. (1965) indicated that benthic organisms were an important component of the diet of the juvenile lake trout in Lake Superior.

M. relicta is a primary food of juvenile trout <250 mm in length (Webster et al. 1959; Dryer et al. 1965; Eck and Wells 1986). If mysids are not available, juvenile lake trout eat other crustaceans such as: isopods

(MacCrimmon et al. 1983) and cladocerans (Konkle and Sprules 1986). Secondary crustacean food items include: amphipods such as *P. hoyi* (Dryer et al. 1965; Stewart et al. 1981); *P. affinis* (Ball 1988); *Gammarus* spp. (Webster et al. 1959; Paterson 1968); copepods (Benoit and Power 1981); and decapods (Franz and Cordone 1970).

Aquatic insects are generally next in importance in the annual diet of small lake trout, after crustaceans, even though juvenile lake trout sometimes feed more heavily on terrestrial insects (i.e. Hymenoptera, Coleoptera) during the spring. Diptera, especially the pupae of Tendipedidae and Chironomidae, are the most important aquatic insect food item during the early spring and summer. Dipteran larvae increase in importance during late summer and into the winter, following adult emergence . Ephemeropteran larvae (e.g. mayflies) are the second most important aquatic insects in the diet of juveniles (Paterson 1968; Benoit and Power 1981; Ball 1988).

Fish gradually increase in importance in the annual diet, as the size of juvenile trout increases. Most studies have observed that juvenile lake trout are largely piscivorous by the time they are 250 to 300 mm long. Cottids are traditionally the most frequently occurring fish species in the stomachs of juveniles during early summer and into the winter. The slimy sculpin, *Cottus cognatus*, is still important in the diet of young lake trout in Lake Michigan (Eck and Wells 1986), Lake Ontario (Elrod 1983; Brandt 1985) and Lake Superior (Collins 1985), and in smaller inland waters (Black 1980; Benoit and Power 1981; Ball 1988). The mottled sculpin, *Cognatus bairdi*, and the deepwater sculpin, *Myoxocephalus quadricornis*, also have been reported in the stomachs of lake trout from inland waters and the Great Lakes (Stewart et al. 1981;

Hassinger and Close 1984; Eck and Wells 1986). YOY alewife (*Alosa pseudoharengus*) were the primary food of young lake trout from mid-spring to early winter in Lake Michigan (Stewart et al. 1981; Eck and Wells 1986) and during the summer in Cayuga Lake, New York (Webster et al. 1959). They were of secondary importance, next to the slimy sculpin, in Lake Ontario (Elrod 1983).

Rainbow smelt are an important food item in the diet of larger juveniles (>300 mm TL) in both inland waters where smelt have been introduced and in the Great lakes (Kircheis 1976; MacCrimmon et al. 1983; Hassinger and Close 1984). Larger juvenile lake trout in Lake Superior feed primarily on smelt; however, they are of secondary importance in lake trout diets in lakes Michigan and Ontario (Elrod 1983; Eck and Wells 1986). Benoit and Power (1981) and Ball (1988) reported that the threespine stickleback, *Gasterosteus aculeatus*, and ninespine stickleback, *Pungitius pungitius*, were important food items in the annual diet of juvenile lake trout in small inland lakes in northern Quebec and Ontario (Black 1980). Coregonids, especially the lake herring or cisco (*Coregonus artedii*), become increasingly important in the diet as juvenile lake trout increase in size. Other important coregonids reported in young trout stomachs from inland waters were lake whitefish (*Coregonus clupeaformis*), round whitefish (*Prosopium cylindraceum*) and the mountain whitefish, *Prosopium williamsoni* (Franz and Cordone 1970; Black 1980). The bloater, *Coregonus hoyi*, which was once a major diet item of lake trout in the native Great Lakes fish community, still occurs in juvenile trout from Lake Michigan, but its original importance has been greatly reduced (Eck and Wells 1986). Small burbot (*Lota lota*) and lake trout often appear in the diet of juveniles in late summer, fall and winter. A variety of shallow water species such as yellow perch (*Perca flavescens*), johnny darter (*Etheostoma nigrum*),

and the spottail shiner (*Notropis hudsonius*) are also eaten during the late fall - late spring period.

ADULTS

Generally, adult lake trout are omnivorous (Fig. 1). Martin and Olver (1980) provided a detailed summary of the adult diet and its changes associated with size, age, and season. In larger lakes and where forage fish are available, lake trout are mainly piscivorous, feeding on a variety of fish species, both introduced and native. Where prey fish are not present, or are seasonally isolated from lake trout by thermal barriers, adult trout rely upon planktonic crustaceans (Konkle and Sprules 1986) and the aquatic larvae of insects (Paterson 1968; Donald and Alger 1986), as primary foods. In homothermous arctic and subalpine lakes, lake trout are less restricted in their movements and seasonal differences in diet are less distinct (Miller and Kennedy 1948; Moshenko and Gillman 1983; Donald and Alger 1986).

In addition to fishing mortality, the quality, quantity and the availability of prey type determines the potential growth patterns of a stock (Kerr 1979; Martin and Olver 1980). Populations which rely on fish for food are characterized by rapid growth and have the potential to achieve trophy size. The absence of pelagic forage fishes (i.e. cisco, smelt, etc.), particularly during the summer period of thermal stratification, has contributed to stunting of lake trout in smaller lakes throughout their range (Martin 1966; Ball 1988). Stunting results from gastric inefficiency (Konkle and Sprules 1986) and the high metabolic demands required to forage for small and dispersed organisms (Kerr and Martin 1970). Lake trout in subalpine Sassenbach Lake, Alberta which fed primarily on insects, were characterized by extremely

slow growth and a limited size distribution (i.e. maximum weight of <500 g at >20 years of age) (Donald and Alger 1986).

In food-limited conditions, adult lake trout may select for larger zooplankton in order to maximize energy intake (Kerr 1971, Konkle and Sprules 1986, Ball 1988). Kettle and O'Brien (1978) suggested that visual predation by lake trout played a significant role in determining zooplankton community structure in arctic lakes. In contrast, Langeland et al. (1989) concluded that lake trout may be considered an inefficient planktivore since no predation effects were apparent on the zooplankton community of Lake Louisa, Ontario. Gregg (1976) suggested that larger food items facilitate more efficient foraging by lake trout due to both their size and tendency to aggregate in the water column.

Predation of smaller trout by larger adults does occur, to some extent, in most populations. The occurrence rate of lake trout cannibalism reported in the literature is extremely varied ranging from 0.0036 in Lake Opeongo, Ontario (Matuszek et al. 1990) to 0.084 in Lac Bonhomme, New Quebec (Benoit and Power 1981). These estimates are probably conservative, owing to the difficulty in identifying partially digested lake trout in stomach contents. Cannibalism appears to be most common during winter (Martin 1970; Ball 1988) and in lakes which lack a diversity of forage species (Martin and Olver 1980). It has been suggested that cannibalism may exist as a primary mechanism of density-dependent population regulation and is a major cause of mortality among juvenile lake trout in populations where adults are abundant, or in lakes where deepwater sanctuary for young trout survival has been lost, due to oxygen depletion during summer (Evans et al. 1990). Young trout which are

normally segregated from adults would be forced into shallower waters, where they would be more vulnerable to cannibalism.

Changes in the Great Lakes fish community brought about by the introduction of the predatory sea lamprey (*Petromyzon marinus*), exotic planktivores (e.g. smelt and alewife), and exotic salmonids have resulted in changes in the diet of lake trout in these lakes. These changes in feeding relationships and community structure have hampered managers' attempts to rehabilitate the Great Lakes. Although a high degree of overlap exists between the food of various salmonids in the Great Lakes, the diets of lake trout tend to be more varied than exotic salmonids.

Coregonids, especially the bloater and the lake herring, and both the slimy and the deepwater sculpins, were originally the mainstay of the diet of adult lake trout in the upper Great Lakes (Van Oosten and Deason 1938; Dryer et al. 1965). Bloaters are now much more scarce in the diet of Great Lakes lake trout, largely reflecting their reduced importance in the fish community. However, as a co-evolved species with lake trout, bloaters may also be less vulnerable to trout predation than recent invaders (Eck and Wells 1986). Alewife are currently the primary food of adult lake trout in lakes Michigan and Ontario during much of the year (Brandt 1985; Eck and Wells 1986). Alewives are important predators on fish larvae and are suspect in having contributed to the collapse of certain native fish populations in the Great Lakes (Crowder 1980; Kohler and Ney 1980). Smelt are also an important dietary component, especially for lake trout larger than 600 mm in length. Busiahn (1985) demonstrated that lake trout growth rates in western Lake Superior

were lower during the 1970s when the diet was dominated by smelt, than in the 1950s when lake herring was the major food item.

FORAGE INTRODUCTIONS

Planned or unintentional introductions of prey species into inland waters, other than the Great Lakes, have also resulted in a variety of impacts on resident lake trout communities. Lake trout are typical inhabitants of oligotrophic lakes, and these lakes are considered to be more sensitive or vulnerable to species introductions than eutrophic lakes (Li and Moyle 1981).

The opossum shrimp, *M. relicta*, has been introduced outside of its native range into many North American and Scandinavian lakes as a supplementary food source for fish. Numerous studies report enhanced survival and growth of juvenile lake trout following such introductions (Wydoski and Bennett 1981; Lasenby et al. 1986). However, mysids which are planktivores have had a detrimental effect on the native zooplankton community, especially cladocerans (Morgan et al. 1978). This has led to decreases in the abundance of pelagic fish species which are dependent on cladocerans for food such as Arctic char, *Salvelinus alpinus*, and whitefish, *Coregonus* spp., in Scandinavian lakes (Lasenby et al. 1986) and kokanee salmon, *O. nerka*, in western North American lakes (Wydoski and Bennett 1981; Martinez and Bergersen 1989). Declines in length and condition of adult lake trout have been observed in response to declines in kokanee, the principal forage of lake trout in Priest Lake, Idaho (Wydoski and Bennett 1981). Although lake trout in Lake Tahoe, California, ate mysids instead of traditional food items, no significant improvement in lake trout condition resulted (Morgan et al. 1978). Once introduced into a lake,

mysids can readily move downstream and disperse throughout a watershed (Martinez and Bergensen 1989).

Lake herring, which were introduced into Lake Opeongo, Ontario in 1948 to improve the forage base of lake trout, especially during the transition in diet from small yellow perch to lake whitefish and larger prey items, have had significant effects on lake trout biology and the lake trout fishery in that lake (Martin 1970; Martin and Fry 1972). Growth rates, condition and fecundity of Lake Opeongo lake trout all increased after cisco became established as the dominant food item (Martin 1970). However, the age and size at maturity were delayed, the average weight of angled trout almost doubled, and the percentage of immature lake trout in the angling catch increased over the long term (Martin and Fry 1972). Initial declines in abundance of yellow perch and invertebrate fauna had recovered by the 1960s. Although the initial growth increase in most age groups of lake trout has since declined, an observed increase in trout abundance, due to increased reproductive efficiency, has remained. This has resulted in a larger sustainable angling catch of lake trout than in the early years of this fishery (Shuter et al. 1987; Matuszek et al. 1990).

Unauthorized introductions of rainbow smelt have occurred in over 60 lake trout lakes, inland from the Great Lakes, in Ontario (Evans and Loftus 1987). Most have resulted in the eventual dominance of smelt in adult lake trout diets along with increased trout growth and condition. However, smelt introductions into small lakes have also led to an observed decline in juvenile lake trout growth since both species compete for the same foods (Hassinger and Close 1984; Evans and Loftus 1987) and to an increase in

mercury concentrations in lake trout, following a switch to smelt in the diet (MacCrimmon et al. 1983). Although smelt were not implicated in the eventual collapse of lake trout in Lake Simcoe (Evans and Waring 1987), they are suspect in the recruitment failure of lake whitefish in this, and several other lakes, following their introduction. Evans and Loftus (1987) recommended that smelt should not be introduced into lakes containing naturally reproducing cold and cool-water species (e.g. lake whitefish and lake trout), as they are capable of competing with, or preying upon earlier life stages of these species.

MANAGEMENT IMPLICATIONS

Most studies indicate that lake trout, at all life stages, are omnivorous, opportunistic feeders, capable of foraging in a variety of habitats on whatever food items are most readily available. It is the quality, quantity, and availability of prey type, together with fishing mortality that determine the potential growth patterns of a stock and account for the observed size composition of the lake trout population. Populations which rely on fish for food are characterized by good growth and have the potential to reach trophy size. In the absence of pelagic forage fishes, particularly during the summer period of thermal stratification, lake trout are forced to become less efficient feeders on planktonic crustaceans and the aquatic larvae of insects. As a result, these populations are slower growing, earlier to mature and shorter lived.

Managers, when faced with increasing demand for angling opportunities in food-limited environments, have tried to enhance growth by introductions of exotic prey species. The negative impacts of prey species introductions

(mysids, cisco, smelt, alewife) on the lake trout community have far outweighed the occasional observed benefit. Ryder and Kerr (1984) considered mysids and ciscoes to be low-risk candidates for introduction as they have co-evolved with lake trout in glacial refugia and display a high degree of niche complimentarity. However, the results of cisco and mysid introductions have been unpredictable and often destructive to native lake trout and other aquatic organisms. Introductions of exotic planktivores (smelt, alewives) have resulted in changes to the zooplankton community structure and have the potential to impact planktonic crustaceans which are the primary food of YOY and juvenile lake trout. While adult lake trout are able to adjust to resulting changes in forage base composition and availability, native fish species, especially whitefish and ciscoes which occupy a similar niche as introduced planktivores, have declined. Finally, changes in diet accompanying community structure alterations may also affect angler preference. In lakes where adult lake trout prey largely on smelt and alewife, anglers complain that lake trout have a strong taste, oiliness, abnormal flesh coloration and high contaminant levels.

Management for trophy lake trout opportunities would only seem practical in larger lakes with abundant native forage fish. There exists a need to further evaluate lake trout growth and harvest properties in relation to dietary patterns and forage availability. We recommend that fisheries managers discontinue the practice of introducing food items to increase lake trout growth and prevent unintentional introductions of exotic food items into lake trout communities.

LAKE TROUT HABITAT

LAKE TROUT SPATIAL DISTRIBUTION AND PHYSIOLOGY

Temperature and oxygen are fundamental controlling and limiting factors of the lake trout environment that are potentially lethal at their extremes (Fry 1947, 1971; Ryder and Edwards 1985). Controlling factors govern the overall rate of metabolism, whereas limiting factors affect activity when in short supply.

Numerous investigators have attempted to determine the physiologically tolerable and preferred or optimum levels of temperature and oxygen for a variety of fish species through controlled laboratory experiments. However, although exact physiological data are essential to our understanding of a species' habitat requirements, laboratory data are often difficult to reconcile with observations of distribution in wild populations because of the many uncontrolled variables in nature. In addition, exact physiological data are not always available for all life stages. To achieve a better understanding of the lake trout's temperature and oxygen requirements in the wild, we examined field observations of lake trout spatial distribution (Table 1) in light of our knowledge of lake trout physiology.

Lake trout sac fry generally emerge from the spawning shoal substrate around late April-early May. Swim-up usually occurs shortly after the beginning of spring overturn when water temperatures are still low (4.5 - 10.0^{o}C) and oxygen concentrations are high (10.0 - 11.6 mg L^{-1}) (Greeley 1936; Royce 1951; Bradbury 1979; Boraski and MacLean 1981). However, these life stages are not easily sampled and there is little information on the distribution of lake trout YOY after this date. Most investigators agree that alevins leave the

shallow water around the end of May (Royce 1951; Martin 1957; DeRoche 1969; Nester and Poe 1984). Peck (1982) observed that young lake trout in Lake Superior stayed in the vicinity of spawning shoals for up to 12 weeks; moving to deeper waters as the temperature approached 15°C. This observation can probably be attributed to Lake Superior's slow rate of warming. After moving from the shallow water, lake trout YOY apparently concentrate at intermediate depths in the hypolimnion (15-50 m) (Greeley 1929; Eschmeyer 1956; J. Segelby, U.S. Fish Wildl. Serv., Nat'l. Fish. Centre, Ann Arbour, MI 48105, pers. comm.; J. Weber, Mich. Dept. Nat. Resour. (MDNR), Alpena, MI 49707, pers. comm.).

Juvenile lake trout often occur deeper in the water column than adults, regardless of season; apparently at temperatures below the 10 - 16°C juvenile lake trout growth optimum (Tompkins 1951; Martin 1952; Eschmeyer 1956; Elrod 1983; Evans et al. 1990; J. Weber, MDNR, pers. comm.).

In the spring, prior to the onset of stratification and the concurrent warming of surface waters, adult lake trout are usually widely distributed in the water column at temperatures ranging from 5.6 - 13°C (Martin 1952; Rawson 1961; Galligan 1962). However, by late June, they are generally found much deeper in the water column, but at similar temperatures. This migration is probably a true temperature response, as oxygen concentrations in surface waters at this time are high. For example, migration from shallow White Trout Lake, Ontario to a deeper, adjacent lake was initiated at temperatures between 9 - 12°C (Kennedy 1941). The migration was largely completed at 17 - 18°C. Larger lake trout moved first. Lake trout in Redrock Lake, Ontario and Lac la

Table 1. Summary of observations on the distribution of lake trout sac fry (SAC), alevins (ALV), young of the year (YOY), juveniles (JUV), and adults (ADL) with respect to depth, oxygen, and temperature. Depth, oxygen and temperature ranges cited reflect zones of abundance.

Life Stage	Lake Location	Season	Depth (m)	Oxygen (mg/l)	Temperature (°C)	Reference
SAC	Otsego Lake, New York	early May	in substrate		6.7	Greeley 1936
SAC	Otsego Lake, New York	late April - mid May	in substrate		6.7	Royce 1951
SAC	Devil Lake, Ontario	late April - May	1.5 - 3.0	11.6	peak emergence 8.0 - 10.0	Boraski and MacLean 1981
SAC	Kushog Lake, Ontario	late April - May	0.8 -1.1	10.0	peak emergence 9.0	Bradbury 1979
ALV	Lake Michigan	April - May	3.0 - 7.0		4.5 - 8.5	Nester and Poe 1984
ALV	Algonquin Park lakes	mid May	fry had left shallows			Martin 1957
ALV	New York State lakes	late May	fry had left shallows		12.7	Royce 1951
ALV	Maine lakes	early May late May	near shoals 18.2 - 30.5		7.8 - 10.0	DeRoche 1969
YOY	Lake Superior	May - July < 12 weeks	2.0 - 12.0		fry move deeper at 15.0	Peck 1982
YOY	Lake Superior	June - August October	< 37 37 - 53			Eschmeyer 1956
YOY	Lake Superior	May - August fall	10 - 15 > 25			Segelby (pers. comm.)
YOY	Hemlock Lake, New York	fall	18.3			Greeley 1929
YOY	Haliburton area, Ontario	summer	30 - 35			Casselman (pers. comm.)
YOY	Lake Michigan	June - October	15 - 21			Weber (pers. comm.)
JUV	Lake Michigan	July - October	peak: 37 - 72			Eschmeyer 1956
JUV	Lake Michigan	May - June July - September	30 30 - 45 (deeper than adults)		4.4 - 7.2	Weber (pers. comm.) Weber (pers. comm.)
JUV	Lake Ontario	late July	20 - 45		4.0 - 6.2	Elrod 1983

Table 1. (continued)

JUV	Georgian Bay		82 - 128 37 - 46			Tompkins 1951
JUV	Redrock Lake, Ontario	early June late June late July	1.5 - 13.7 10.6 - 16.8 4.6 - 12.2 (lake trout < 25 cm generally deeper than adults)		6 - 13 6 - 12 8 - 18	Martin 1952
ADL	Louisa Lake, Ontario	early July late July mid August	9.1 - 18.3 24.4 - 30.5 6.1 - 48.8	4 - 5 presumably sufficient	8 - 10 8 8 - 10	Martin 1952
ADL	Lac La Ronge, Saskatchewan	early June July - August mid - September	5 - 30 25 - 35 0 - 2		6 - 10 8 - 10 13	Rawson 1961
ADL	Lac La Ronge, Saskatchewan	mid summer	15 - 35	lake trout move up at 3.6 - 4.3	8 - 10	Rawson and Atton 1953
ADL	Moosehead Lake, Maine	summer	9.1 - 27.4	8.3 - 10.1	10 - 14	Cooper and Fuller 1945
ADL	Alluring Lake, Ontario	mid summer	10 - 18	5.9 - 8.1	5 - 7	Straight 1969
ADL	Cayuga Lake, New York	early June late July mid August	12.2 - 42.7 7.6 - 51.8 16.7 - 45.7		5.6 - 12.8 5.6 - 18.3 5.6 - 12.8	Galligan 1962
ADL	Cayuga Lake, New York	July - August	12.5 - 30		10 - 14	Dahlberg 1981
ADL	Lake Ullevifjarden, Sweden	July October	15 - 25 10 - 25	lake trout move up due to oxygen depletion		Nilsson and Svardson 1968
ADL	Colorado lakes			rarely go below 4		Nolting (unpublished) *

Ronge, Saskatchewan also moved to deeper water as water temperatures reached 14 - 15°C (Martin 1952; Rawson 1961).

Adult lake trout apparently remain in these deeper waters throughout July and August, at temperatures usually ranging from 5.6 - 14°C (Cooper and Fuller 1945; Rawson and Atton 1953; Nilsson and Svardson 1968). Periodic excursions into the warm epilimnion (>16°C) have been attributed to feeding behavior (Cooper and Fuller 1945; Straight 1969; Dahlberg 1981; Table 1).

In general, lake trout at all life stages are distributed below the 15°C isotherm and above the 4 mg L^{-1} oxygen isopleth. As the environment approaches these threshold values, lake trout move up or down in the water column depending on whether temperature or oxygen is the more critical stressor. However, the mean median temperature selected by adult lake trout in various field studies (Table 1) was 9.66 $\pm$ 1.09°C.

There is also evidence that juvenile lake trout live deeper in the water column, at cooler temperatures than adults. The mean median temperature selected by juvenile lake trout in field studies that we reviewed (Table 1) was 5.87 $\pm$ 1.98°C. Evans et al. (1990) hypothesized that juvenile lake trout may occupy deeper water to avoid predation by adults.

Although there is little known about the sublethal limiting effect of oxygen on lake trout physiology, Brett (1979) stated that, in general, an oxygen concentration of at least 5 mg L^{-1} is critical for growth; a drop of 1 mg L^{-1} causing a 30% reduction in growth rate. In his review of sublethal oxygen effects, Davis (1975) determined that freshwater salmonid respiratory

functions are affected at oxygen levels below 57.6% saturation (6.3 mg L^{-1} at 10°C). Magnuson et al. (1979) reviewed dissolved oxygen criterion for the Great Lakes and recommended that dissolved oxygen level should not be less than an average of 6.5 mg L^{-1}, nor less 5.5 mg L^{-1} at any time over 24 hours and across a temperature scale of 0 to 25°C.

Evans et al. (1990) estimated the mean median upper (5.8 $\pm$ 0.5 mg L^{-1}) and lower (4.2 $\pm$ 0.6 mg L^{-1}) oxygen response thresholds for adult lake trout. The upper response threshold indicates the average oxygen concentration at which swimming activity initially increases in response to declining oxygen. The lower oxygen response threshold is the average oxygen concentration at which lake trout show an avoidance response.

Gibson and Fry (1954) determined that the upper incipient lethal temperature and oxygen level for no excess activity other than standard metabolism for juvenile lake trout were 23.5°C and 2.8 mg L^{-1} oxygen (at 10°C). In their review of dissolved oxygen requirements, Doudorff and Shumway (1970) observed that for other coldwater species, direct lethal effects begin at around 3 mg L^{-1} oxygen. Evans et al. (1990) showed that if minimum summer oxygen concentrations were <3.1 and 2.3 mg L^{-1} for adult and juvenile habitat, respectively, populations would likely be lost.

THE OPTIMUM AND USEABLE HABITAT MODEL

The Ontario Ministries of the Environment and Natural Resources recently co-developed habitat models based on "optimum" and "useable" habitat volumes that predict the effects of nutrient input from shoreline development on the oxygen and temperature regimes of lake trout waters in Eastern Ontario (OMOE

and OMNR 1986; OMOE 1987). That volume of a lake with an upper temperature limit of 15.5°C and a lower oxygen limit of 4 mg L^{-1} was defined as "useable habitat" following Martin and Olver's (1976) review of lake trout spatial distribution with respect to temperature and oxygen. "Optimum habitat" was defined as that stress-free volume within the useable habitat volume where neither oxygen nor temperature is limiting. The upper limit of the optimum habitat zone was set at 10°C (after Scott and Crossman 1973); the lower at 6 mg L^{-1} oxygen (after OMOE 1978). These same two habitat volume constructs were used by Evans et al. (1990) who referred to optimum lake trout habitat as "preferred habitat"; and useable lake trout habitat as "vital habitat". Although a more detailed rationale for these two habitat constructs has not been developed, they appear valid in light of physiological and spatial distribution data.

OPTIMUM AND USEABLE HABITAT AND LAKE TROUT REPRODUCTIVE STATUS

If optimum and useable habitat are good indicators of lake trout habitat suitability, population status should be related to these constructs. We established a data base for 151 lake trout lakes in the Algonquin and Eastern regions of OMNR (Appendix A) to investigate this relationship. The Kingston office of OMOE provided optimum and useable habitat volumes standardized to August 31 for Eastern Region lakes. We calculated Algonquin Region habitat data using seasonal OMOE water quality profiles and depth contour information from the OMNR Aquatic Habitat Inventory. Optimum and useable habitat volumes were calculated for each sampling period between May and September and the individual values plotted. Standardized habitat volumes were interpolated to August 31. To ensure consistency, optimum habitat volumes for several Algonquin Region lakes were recalculated using the OMOE, Kingston program.

Lake trout reproductive status for each of the above waters was assigned according to the classification provided in Evans et al. (1990) and confirmed by OMNR districts. Most of the lakes in our data set are in five reproductive categories:

N1 - Native population, natural reproduction, self sustaining, unstocked;

N3 - Native population, natural reproduction, partly self sustaining, supplemented by plantings of non-native stock;

N5 - Native population, little or no natural reproduction, population maintained by plantings of non-native stock;

I2 - Introduced population, no native stock, population maintained by plantings; and

E - Extinct population, native or introduced population which disappeared from a lake after a known period of natural reproduction.

Introduced lake trout populations with no native stock (I2) were not included in the final analysis. These lakes were originally chosen for stocking partly on the basis of their suitable oxygen and temperature regimes. The failure of these introduced lake trout populations to reproduce is likely controlled by factors other than water quality, (i.e. the absence of appropriate spawning areas).

A new population status category (I3) was created (after Evans et al. 1990) to include introduced populations with no native stock which are partly self-sustaining, but still supplemented by plantings of non-native stock. This category is analogous to the N3 grouping on native lake trout lakes.

Initially, 5x5 contingency tables of percent total volume and population status were constructed for both optimum and useable habitat. The various

population status categories were arranged with respect to their ability to sustain themselves by natural reproduction. A chi-square test was used to determine whether percent optimum and useable habitat were associated with population status. Basic descriptive statistics were then generated to describe the distribution of optimum and useable habitat (expressed as a percentage of total lake volume) for lake trout lakes within each reproductive category. Each distribution was tested for normality.

A one way analysis of variance (ANOVA) was used to test the normally distributed useable habitat data for differences between groups. The optimum habitat data were not normally distributed and included a large number of zeros. A square root transformation $(Y+.5)^{.5}$ was unable to restore normality. A Kruskall-Wallis test was used to test the untransformed data. Significant differences between individual population groups were determined using the Newman-Keuls and Mann Whitney U tests (Siegel 1959; Zar 1974). Unless otherwise stated, all statistical tests were at the 95% confidence level.

The distribution of optimum and useable habitat for each of the five population categories is shown in Table 2. Several trends are readily apparent:

N1 lake trout lakes are generally characterized by high levels of optimal and useable habitat. However, almost 21% of these waters have zero optimum habitat.

N3 lake trout lakes are similarly characterized by high levels of optimal and useable habitat. There is a lower percentage of N3 lakes with zero optimum habitat (compared to N1 lakes).

N5 lake trout lakes are characterized by low levels of optimum habitat and high levels of useable habitat.

The percentage optimum habitat for I3 lake trout lakes is more or less equally distributed over intermediate to high levels. Eighty one percent (81%) of I3 lakes have >30% useable habitat.

Lakes in which lake trout have disappeared (category E) are characterized by low levels of both optimum and useable habitat (76.9% extinct lakes have zero optimum habitat; 46.2% have zero useable habitat).

Lake trout have not become extinct in lakes with >20% optimum habitat.

Lakes with zero useable habitat do not exhibit significant natural reproduction of lake trout.

Table 2. Distribution of optimum and useable habitat volumes (expressed as a percentage of total lake volume) for five lake trout population categories. See text for population status definitions. ( ) denotes percent of column total.

	Population status				
Percent optimum habitat	N1	N3	I3	N5	E
0	6(21.4)	6(10.5)	1(9.1)	12(50.0)	10(76.9)
0 - 10	1(4.2)	5(8.8)	2(18.2)	3(12.5)	1(7.7)
10 - 20	4(16.7)	10(17.5)	3(27.3)	4(16.7)	2(15.4)
20 - 30	2(8.3	8(14.0)	2(18.2)	1(4.2)	0(0.0)
30 - 100	15(62.5)	28(49.1)	3(27.3)	4(16.7)	0(0.0)
Totals	28	57	11	24	13

	Population status				
Percent useable habitat	N1	N3	I3	N5	E
0	0(0.0)	0(0.0)	0(0.0)	2(8.3)	6(46.2)
0 - 10	3(10.7)	3(5.3)	0(0.0)	2(8.3)	0(0.0)
10 - 20	1(3.6)	2(3.5)	1(9.1)	7(29.2)	2(15.4)
20 - 30	3(10.7)	4(7.0)	1(9.1)	2(8.3)	4(30.8)
30 - 100	21(75.0)	48(84.2)	9(81.8)	11(45.8)	1(7.7)
Totals	28	57	11	24	13

Chi-square tests showed a significant association between both percent optimum and useable habitat and population status (X^2 optimum = 43.779, df. = 16; X^2 useable = 73.912, df. = 16). However, there is a question as to the validity

of this X^2 test due to the nature of the data. Cochran (1954) recommended that fewer than 20% of the cells in a X^2 test have an expected frequency of less than 5 and that no cell has an expected frequency equal to zero. When greater than 20% of the cells have an expected frequency of less than 5, adjacent cells are to be pooled. Although we lose some of the meaning of our original data by pooling classes, there is no alternative statistical test. Nevertheless, the pooled contingency table is still significant (X^2 optimum = 19.087, df. = 4; X^2 useable = 35.428, df. = 4).

The Kruskall-Wallis test demonstrated that there was a significant difference in mean optimum habitat ($H_{corrected}$ = 38.13, df.= 5) between reproductive categories. Mann Whitney U tests divided the categories into two groups. There was a significant difference in median optimum habitat between lakes where significant natural reproduction was present (N1,N3,I3) and those lakes where natural reproduction was severely impaired or absent (N5,E) (Table 3).

Table 3. Results of Mann Whitney U tests for significant differences in optimum habitat volume (expressed as a percentage of total lake volume) between lake trout lakes of different population status. Any two samples not underscored by the same line come from populations with different distributions.

Population status	N3	N1	I3	N5	E
Optimum habitat (mean)	31.9	28.9	24.0	10.2	2.8
(median)	29.5	32.4	20.0	1.1	0.0

A one-way analysis of variance also demonstrated a significant difference between reproductive categories for mean useable habitat ($F_{5,150} = 12.17$). Newman-Keuls multiple range tests divided the categories into three groups:

lakes with significant natural reproduction (I3,N1,N3); remnant populations with little or no reproduction (N5) and those lakes which have already lost their lake trout populations (E) (Table 4).

Table 4. Results of Newman-Keuls multiple range tests for significant differences in mean useable habitat volume (expressed as a percentage of total lake volume) between lake trout lakes of different population status. Any two means not underscored by the same line are significantly different.

Population status	I3	N3	N1	N5	E
Mean useable habitat	52.6	48.7	42.1	26.5	13.6

Nevertheless, it is important to keep in mind that we are testing for differences in population means and medians. Although optimum and useable habitat levels tend to be higher in naturally reproducing populations and lower in populations where reproduction is impaired, there is one obvious exception. Almost 21% of N1 lake trout lakes have zero optimum habitat.

The relationship between optimum habitat and useable habitat for all lake trout lakes in our data set is shown in Fig. 2. The resulting plot exhibits increasing scatter as optimum habitat declines. Several factors account for this increasing variation. Lakes with great depth and volume or small surface area often do not mix very deep during spring overturn and enter summer stratification with less than saturated conditions in the hypolimnion. These lakes generally have low levels of optimum habitat while the volume of useable habitat on a particular lake varies with the degree of mixing and concentration of nutrients. Other lakes with shallow mean depth, great surface

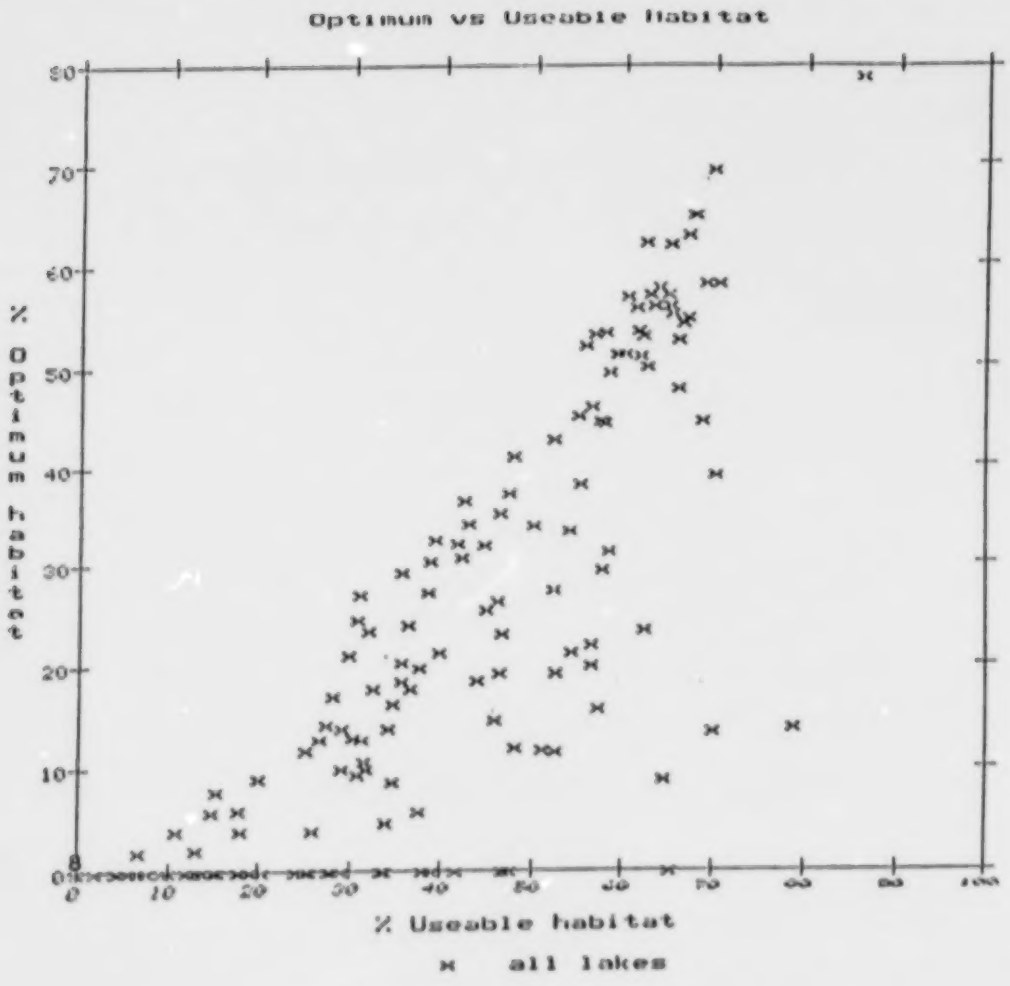


Fig. 2. Relationship of optimum habitat to useable habitat for 151 lake trout lakes.

area and long fetch, often continue mixing until the temperature of the entire water column is several degrees above 4°C (Wetzel 1975) and most optimum habitat is gone. The volume of useable habitat remaining again depends upon the degree of mixing and nutrient input. Martin and Olver (1976) reported that 86% of lake trout lakes have a mean depth greater than 6.1 m. The 14% of lake trout lakes with a mean depth of less than 6 m are likely predisposed to low optimum habitat levels.

The relationship between optimum and useable habitat is shown separately for each reproductive category in Fig. 3. The number of waters with impaired reproduction or extinct lake trout populations increases towards the origin. Most extinct (E) and remnant (N5) lake trout lakes are found below approximately 20% optimum habitat and 40% useable habitat. Furthermore, the majority of N1 and N3 lake trout lakes and almost all introduced lake trout lakes that now support natural reproduction are located outside of this zone (20% optimum habitat, 40% useable habitat). Nevertheless, there are 25 N1 and N3 lakes with <20% optimum habitat and 40% useable habitat.

Upon closer examination, several features of this set of 25 naturally reproducing lakes are evident (Table 5). First, most of the lakes have a small surface area (mean = 181.6 $\pm$ 83 ha) which makes them susceptible to poor spring mixing. Second, OMOE and OMNR (1986) have identified all eight Eastern Region lake trout lakes in this zone as "highly sensitive" to additional input of nutrients, (i.e. the lakes lose greater than 50% of their optimum habitat after a 100 kg phosphorous input). Further, two of the lakes (Little Black and Eyre) contain the unique Haliburton lake trout strain which is apparently distributed over a greater within-lake temperature range than most other Ontario populations (J. Casselman, OMNR, Glenora Fisheries Station, Picton, Ont. K0K 2T0, pers. comm.). These lake trout may be better adapted to low optimum habitat conditions than other stocks.

We propose 20% optimum habitat and 40% useable habitat as an "incipient limiting" habitat volume below which lake trout populations have a reduced reproductive potential and abundance. Zero percent useable habitat would

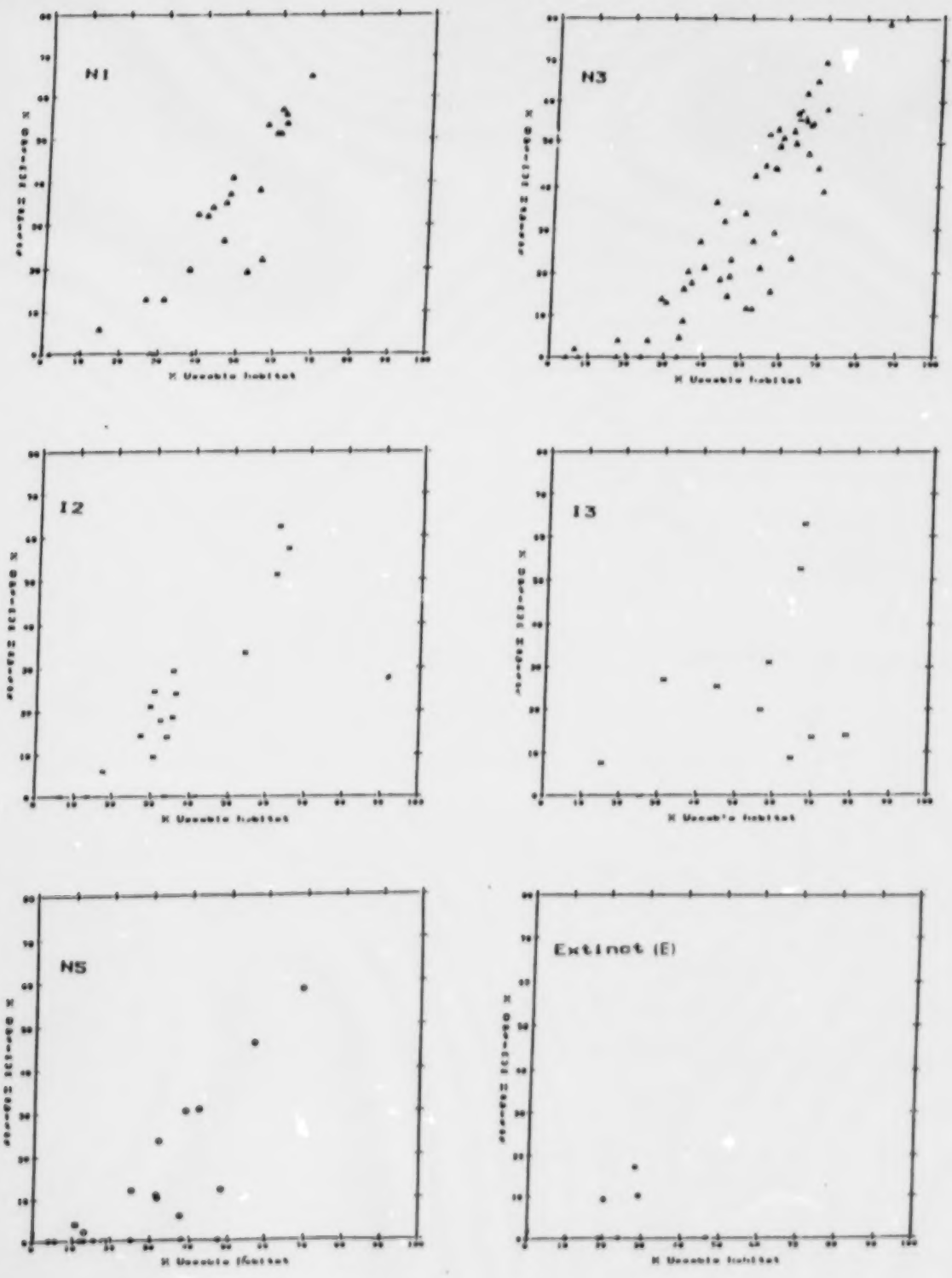


Fig. 3. Relationship of optimum habitat to useable habitat for each reproductive category.

correspond to an "incipient lethal" habitat level. Lake trout populations can apparently maintain some lower production level below 20% optimum habitat as long as useable habitat levels are high and stress levels are low. It appears that if stress levels were to increase on these lakes, their reproductive status would soon deteriorate. The most likely stresses to impact on the lake trout populations in these lakes are exploitation and cultural eutrophication.

Table 5. Summary of information for N1 and N3 lake trout lakes with less than 20% optimum habitat and 40% useable habitat.

Lake	District	Surface area (ha)	Volume ($m^3 \times 10^6$)	Percentage optimum habitat	Percentage useable habitat	LT origin
Art	54	126.3	9.60	0.0	2.0	N1
Ashden	66	138.0	13.69	16.4	34.6	N3
Clinto	53	137.6	11.05	1.9	6.7	N3
Deer	52	189.7	16.04	0.0	24.2	N3
Delano	51	26.1	1.70	0.0	0.0	N1
Delphis	54	26.4	2.67	12.9	26.6	N1
Dickson	51	975.0	53.60	0.0	0.1	N1
Eyre	54	65.6	5.19	12.9	31.2	N1
Hudson	52	73.7	8.22	13.0	30.3	N3
Joe Perry	66	169.0	12.35	0.0	33.5	N3
Little Black	54	21.9	1.66	5.8	14.8	N1
Long	52	95.5	8.96	0.0	39.0	N1
Loon	53	31.5	1.57	0.0	4.6	N3
Lucky	66	100.0	11.82	14.0	29.1	N3
Silent	52	118.3	7.67	0.0	20.5	N3
MacDonald	54	137.8	14.97	19.8	37.5	N1
Mackie	66	158.0	13.74	4.7	33.9	N3
Marsden	54	230.2	8.76	0.0	9.3	N1
Mountain	52	143.4	2.13	0.0	7.6	N3
Reid	66	105.0	8.00	0.0	17.8	N3
Salmon	54	171.9	19.74	17.8	36.5	N3
Sharbot (West)	66	684.0	63.83	4.0	25.8	N3
Thanet	66	112.0	8.76	4.0	18.0	N3
Timberwolf	51	167.0	11.70	0.0	0.0	N1
Twelve Mile	54	336.8	40.87	8.7	34.6	N3

LAKE TROUT OPTIMUM AND USEABLE HABITAT AND SPORT FISHING HARVEST

Christie and Regier (1988) developed a model to relate the sustained commercial yield of northern pike (*Esox lucius*), walleye (*Stizostedion vitreum*), lake whitefish, and lake trout in large lakes to a thermal habitat volume (THV). Across the 15 lakes in their data set, they found that 86% of the variation in lake trout yield was explained by THV. The THV concept closely parallels optimum and useable habitat (OMOE and OMNR 1986), but has two major differences. First, the "habitat" volume defined is based on temperature alone (i.e. that volume between 8 and 12°C). Second, the data requirements necessary to calculate THV are quite rigorous, limiting its utility to managers. However, Payne et al. (1990) determined that these requirements can be substantially reduced.

We have already shown that there is an association between optimum and useable habitat and lake trout reproductive status. We used the data base assembled by Goddard et al. (1987) as a starting point for our investigation into the relationship between optimum and useable habitat and lake trout sport fishing harvest. Optimum and useable habitat data were only readily available for 26 of the original lakes. Partial correlation and multiple linear regression analyses of lake trout harvest (expressed in kg) were carried out following $\log_{10}$ transformation of all the data.

Table 6 shows the partial correlations of selected variables with harvest before they are entered into the multiple regression. 'Multiple R^2' is the change in R^2 that would take place if the variable in question was added to the model. 'F-to-enter' tests whether that variable adds significantly to the model. 'Significance' shows the significance of the test.

Table 6. Partial correlation and multiple R^2 values for area, volume, morphoedaphic index, useable habitat volume, optimum habitat volume and effort before they are entered into the multiple regression model against harvest. See text for explanation of headings.

Variable	Partial correlation	Multiple R^2 to enter	F to enter	Significance
Area	0.831	0.690	51.27	0.00010
Volume	0.869	0.756	71.11	0.00010
MEI	0.089	0.008	0.18	0.67356
Useable habitat	0.874	0.763	74.11	0.00010
Optimum habitat	0.767	0.589	32.96	0.00010
Effort	0.937	0.877	16.196	0.00010

Effort was most highly correlated with harvest (r = 0.937) followed by useable habitat volume (r = 0.874); volume (r =.8699); area (r = 0.831); optimum habitat volume (r = 0.767) and MEI (r = 0.089). Goddard et al. (1987) also observed that lake trout catch was poorly correlated with MEI and attributed the poor correlation in their data set to the lack of contrast in MEI values. Although optimum habitat would significantly add to the model if it were the only variable added (F = 32.96 at 0.0001 level); it was not as useful a predictor of harvest as effort, useable habitat, volume and area.

Multiple regression analyses determined that effort and useable habitat are the best predictors of lake trout annual harvest (Table 7). The relationship was:

$$\log Y = .40(\log UH) + 0.77(\log EFF) - 1.90;$$

where Y = annual harvest of lake trout (kg);

UH = useable habitat volume ($m^3 \times 10^6$);

EFF = angling effort directed towards lake trout (angler-hours).

Although lake trout harvests on these inland waters are largely determined by effort, they are also related to the useable habitat volume.

Table 7. Analysis of variance table for the multiple stepwise regression of effort and useable habitat volume against harvest.

Source	Sum of squares	Degrees of freedom	Mean square	F value	Significance
Regression	72.947	2	36.474	124.290	0.0001
Residual	6.456	22	0.293		

MANAGEMENT IMPLICATIONS

The optimum and useable habitat concepts provide a connection between water quality models and lake trout populations. Fisheries managers can use the association between optimum and useable habitat to select lakes where rehabilitation or introduction attempts will meet with most success. More importantly, managers can easily identify lake trout waters that apparently require an extra measure of protection if they are to support self-sustaining populations.

Further research is needed into the underlying mechanisms limiting recruitment, reproduction and abundance before we can better define "critical" lake trout habitat and understand the role of different stresses. Evans et al. (1990) have hypothesized that recruitment may be controlled through the loss of oxygen in the hypolimnetic waters which forces juvenile lake trout to move higher in the water column where they are subject to increased predation by adults. The nearshore effects of nutrient loading on spawning areas can limit reproduction. In general, good relative abundance estimates were lacking for

most of the inland lake trout populations in our data set; particularly the smaller lakes. Moreover, traditional creel surveys provide unreliable estimates on these low pressure fisheries. New, precise, yet inexpensive methods of estimating lake trout abundance are needed.

OMOE and OMNR (1986) developed a model to predict the percentage loss in optimum habitat after a 100 kg increase in phosphorous. They proposed that shoreline development be discontinued on lake trout lakes that lose >50% of their optimum habitat; while restricted development would be allowed to proceed on others. Inherent in this decision, is the assumption that some optimum habitat can be sacrificed without jeopardizing the lake trout fishery. To protect self-sustaining lake trout populations, we recommend that the "incipient limiting" level of optimum habitat (20%) and useable habitat (40%) be adopted as the minimum acceptable habitat volume after nutrient input. If the model predicts that habitat volumes will fall below these levels, shoreline development must not be allowed.

Our investigation into optimum and useable habitat and lake trout harvest gives managers some insight into the role of cultural eutrophication as a stress on lake trout waters and should strengthen the case for restricted shoreline development. In the past, Ontario Municipal Board hearings have sometimes been unconvinced of the harmful biological effects of reduced optimum habitat volumes (R. Genge, OMOE, Kingston, K7P4X6, pers. comm.), but managers can now equate a loss in useable habitat with a potential reduction in lake trout harvest.

LAKE TROUT SPAWNING BEHAVIOUR

Spawning behaviour of lake trout is in sharp contrast to the general pattern for other salmonids (Keenleyside 1979). There is no distinct sexual dimorphism or colouration associated with spawning of lake trout (Martin and Olver 1980); little or no obvious aggression among males (Martin and Baldwin 1960; Noakes 1980); no apparent alternate strategy such as small fish spawning with much larger fish, as in Atlantic salmon (*Salmo salar*) (Jones and King 1952); and no nest (redd) construction (Martin and Olver 1980). Except for the latter, these differences appear to be related to another feature of lake trout reproductive behaviour-lake trout appear to be the only salmonid that spawns exclusively at night. Thus, for a nocturnal spawner, there may be little advantage to distinct changes in body shape or colouration, sneaking strategies camouflaged by reduced body size, and aggressive conflicts between males.

Egg deposition in the interstitial spaces of spawning substrate is likely to be an anti-predator strategy, and is particularly appropriate for fishes that provide no parental care of the brood. In most salmonids, egg hiding is done actively through nest construction and burial in the gravel. The lake trout has a more passive strategy of broadcasting negatively buoyant eggs over porous substrate. Spawning at night at cold temperatures may also reduce egg predation.

The uniqueness of lake trout spawning behaviour can be readily seen when contrasted to that of a close relative, the brook trout (*S. fontinalis*). These species cohabit many Ontario lakes. The brook trout displays the classic reproductive pattern of salmonids (colouration changes, aggression and redd construction) (Greeley 1932; Smith 1941). Both species are fall spawners,

although lake trout usually spawn somewhat earlier. They can readily cross fertilize (Berst et al. 1981), but are reproductively isolated by differences in timing and location of spawning. The brook trout spawns during the daylight and excavates redds at sites of upwelling groundwater, rather than depositing eggs over rubble shoals at night. These differences are genetically determined and the hybrid splake, (*Salvelinus namaycush x S. fontinalis*) appears to be intermediate in some of these behavioural patterns. It spawns during both day and night, constructs nests as well as broadcasts eggs over less defined sites, and displays courting behaviour that appears to be a mixture of that of the two species (Berst et al. 1981).

Lake trout move onto spawning sites when water temperatures decline in the fall. In Ontario lakes, most lake trout populations spawn in October (Martin and Olver 1980). Spawning begins slightly before or just after, disruption of thermal stratification, when the water temperature is approximately 10°C. Environmental factors such as accumulated sunlight (Royce 1951; McCrimmon 1958), wind direction and intensity (Martin 1957; DeRoche 1969) and rate of temperature decline appear to affect the timing of migration onto the shoals, as well as the duration of the prespawning activity. The spawning period may vary from a few days to nearly a month in duration (Martin and Olver 1980).

Males usually precede females to the spawning shoals each year. This fact, plus the earlier maturation of males (1-2 years) leads to a highly skewed sex ratio on the spawning grounds (Martin and Olver 1980). There is little information available to explain why males arrive at the spawning sites before females (often 5-10 days). They do not appear to establish territories during this prespawning congregation, at least no marked aggression is seen between

males (J. Gunn, OMNR, pers. observations). One can speculate about the possible need to synchronize gonad maturation, or to mark sites to attract females, but these aspects of spawning behaviour have not been investigated.

There is considerable evidence that very specific sites are used for spawning and that some sites are used year after year (Martin 1960; Ball 1988). What remains in question however, is whether individual fish exhibit a fidelity to a single site. MacLean et al. (1981) and Peck (1986) have shown that individual fish visit more than one site during the spawning period and that females travel more than males (MacLean et al. 1981). However, it is uncertain whether female lake trout that travel to several sites are actually using these sites, or if this movement is part of a "proving behaviour" during which sites, or perhaps, groups of males, are inspected before a site or group is chosen.

It is also uncertain how traditional (i.e. frequently used) spawning sites are found when a fish reaches maturity. Foster (1985) showed that lake trout can use olfactory and/or gustatory cues (pheromones) to locate spawning substrates containing conspecific odours/tastes. Bile fluids have proven to be powerful attractants to Arctic char; a closely related species (Doving et al. 1980; Selset and Doving 1980). Foster (1985) suggested that lake trout may use chemosensory cues which originate from waste products deposited by adults, or from decomposing egg shells and dead embryos (on the site from the previous year) to locate spawning sites. This pheromone hypothesis was developed from experimental studies in the laboratory and has not yet been verified in the wild. However, it is unlikely that smell will provide the full answer because

lake trout move great distances between spawning seasons (Walch and Bergersen 1982; Ihssen et al. 1988).

There is little information on sensory perception in lake trout. Some work on thermal preference (McCauley and Tait 1970; Mac 1985) and response to pressure (Tait 1960) have been conducted, but little information exists on senses such as vision (Ali and Wagner 1980), taste, smell, hearing and lateral line sensing, all of which are presumably involved in migration and spawning.

Although we are uncertain about how lake trout select spawning sites, there are physical features that are common to most spawning sites, particularly those in small inland lakes. In Algonquin Park lakes, Martin (1955, 1957) and Martin and Olver (1980) described lake trout spawning sites as having the following characteristics:

Substrate	broken rubble (2-20 cm diameter), clear of detritus, and usually mixed with boulders and patches of gravel (Martin 1955)
Water Depth	0.1 to 5.0 m deep (Martin and Olver 1980)
Wind Exposure	high exposure to prevailing winds and wind driven currents (eg. at shoreline outcroppings, offshore reefs or along windward sides of islands) (Martin 1957)
Bottom Contours	usually found near areas of steep dropoffs. These steep underwater sites are often associated with terrestrial shorelines with bare rock faces (Martin and Olver 1980)

A KEY TO IDENTIFY POTENTIAL SPAWNING SITES OF LAKE TROUT IN ONTARIO INLAND LAKES

In recent years, many lake trout spawning sites have been identified in a large number of inland (i.e. non-Great Lakes) Ontario lakes. These sites were usually identified to protect spawning habitat from shoreline development, or to collect large numbers of fish for population assessments. Investigators

often used the criteria described above to identify spawning sites. However, no assessment has been made to determine which of the commonly reported physical characteristics, stated above, are most useful for locating actual sites.

We collected information on the physical characteristics of known spawning sites in lakes from across Ontario. Our objective was to establish a key or set of rules to allow fisheries managers to predict the likely location of potential spawning sites for lake trout. We restricted ourselves to relatively small inland lakes, where we had the most detailed data. Some information exists for spawning sites on the Great Lakes (Nester and Poe 1984; Peck 1986), but in general, we lacked detailed information on natural spawning sites on these lakes. We also speculated that quite different factors would limit site selection in inland lakes (e.g. minimum fetch for waves to clean site) as opposed to the Great Lakes (e.g. shallow areas affected by ice scour).

Data on lake trout spawning sites were collected by questionnaires sent to OMNR district and fisheries assessment unit biologists, OMNR research scientists, Department of Fisheries and Ocean (DFO) scientists, and selected consultants. The questionnaires provided us with detailed descriptions of each spawning site, general information about the lake, the methods of observation and measurement, and the level of confidence the observers had in their records. Each site was marked on a bathymetric map of the lake. From the maps we measured fetch, and degree of wind exposure (or shelter). A description of the variables used to characterize lake trout spawning habitat is given in Table 8.

Table 8. Description of variables used to characterize lake trout spawning habitat.

Water depth

Min depth - water depth (m) at shallowest part of spawning area
Max depth - water depth (m) at deepest part of spawning area
Mean depth - average water depth (m) in spawning area. (arithmetic mean of min depth and max depth)

Distance to shoreline - distance (m) from shore to edge of spawning area

Fetch - maximum straight line uninterrupted distance that wind driven waves can travel to the site from any direction

Substrate

Rock - exposed flat rock greater than 1 m in diameter
Boulder - rocks 30 cm - 1 m in diameter
Rubble - material 5 cm - 30 cm in diameter
Gravel - material 0.1 cm - 5 cm in diameter
Sand - material of crystalline rock origin less than 0.1 cm in diameter but large enough to feel like grit
Silt - inorganic material of various origins but finer than sand

Orientation to wind

Direction of exposure - compass direction from which wind driven waves can reach the site (assumes that a minimum of 200 m fetch is needed to generate waves)

Data were obtained from 95 inland lakes and for a total of 281 individual spawning sites (Table 9). The number of sites described per lake varied from 1 to 13. The lakes ranged in surface area from 26 ha to 246,718 ha (median = 607 ha). Summary statistics of selected variables in the data set are presented in Table 10.

Table 9. Data sources for lake trout spawning site descriptions.

Region	District	Number of lakes	Number of sites
North Central	Terrace Bay	1	2
Northern	Timmins	1	1
	Kirkland Lake	1	5
Northwestern	Kenora	4	18
Northeastern	Blind River	4	18
	Wawa	1	3
	Sudbury	4	8
	Temagami	5	23
	Sault Ste. Marie	3	4
Algonquin	Algonquin Park	9	38
	Bancroft	17	47
	Bracebridge	3	6
	Minden	11	24
	Parry Sound	3	5
	Leslie M. Frost Centre	3	8
Eastern	Brockville	3	10
	Carleton Place	1	1
	Napanee	8	23
	Tweed	12	36
Totals		95	281

Table 10. Summary statistics of selected variables for all study lakes.

Statistic	Minimum shoal depth (m)	Maximum shoal depth (m)	Mean shoal depth (m)	Distance from shore (m)	Fetch (km)
Mean	0.71	2.47	1.35	14.99	2.96
Median	0.50	2.00	1.00	0.50	2.53
Standard deviation	0.72	1.44	0.86	69.84	1.81
Minimum	0.00	0.18	0.10	0.00	0.47
Maximum	6.00	7.60	6.00	1000	12.35
No. of sites	220	211	234	271	277

We used observed conditions at known spawning sites to develop a set of rules that could be used to classify **POTENTIAL REPRODUCTIVE HABITAT (PRH)** on unstudied lakes. In the following sections the individual mapping rules are described starting with a rule related to water depth. The rules are generally applied in sequence to eliminate areas of the lake where spawning is unlikely to occur. At the end of the key we illustrate the use of the rules with a hypothetical example.

Lake trout spawning sites are located in very shallow water (Table 10). Some sites extend right to the shore and eggs are deposited in as little as 10 cm of water. The mean depth at a site varied from 0.1 m to 6.0 m, with an average of 1.4 m for all sites. In the total sample, 28% of the sites had a mean depth of less than 1 m; 76% less than 2 m; 92% less than 3 m; 98% less than 4 m (Fig. 4).

McMurtry (1986) addressed the question of potential bias in the depth distributions due to the visual method of observing sites (i.e. it is easier to see sites in shallow water). He showed that sites identified visually (n=176), usually by cruising the shores at night with the aid of underwater lights, did not significantly differ in depth from sites (n=25) identified with sonic tracking gear. We propose our first rule for the identification of potential reproductive habitat:

RULE 1: WATER DEPTH PRH = area of the lake with depth <4 m

Most spawning sites were located near shore (Fig. 5). Eighty-three percent (83%) of the identified sites were less than 10 m from the edge of an island or from the perimeter of the lake. We believe this near-shore distribution is

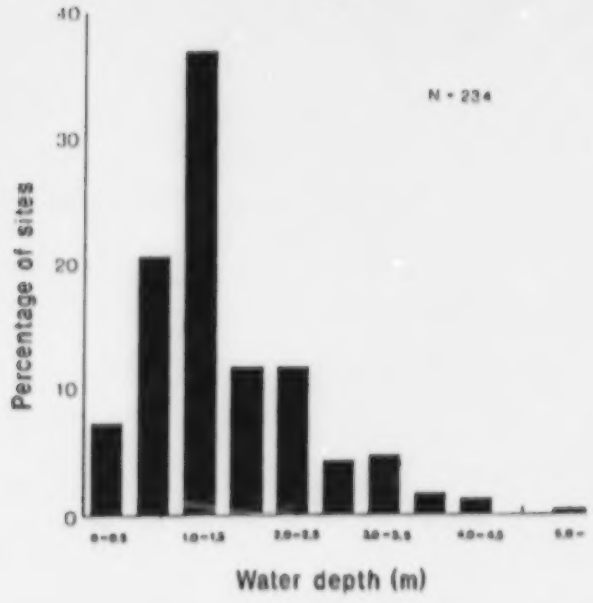


Fig. 4. Water depth at lake trout spawning sites in Ontario.

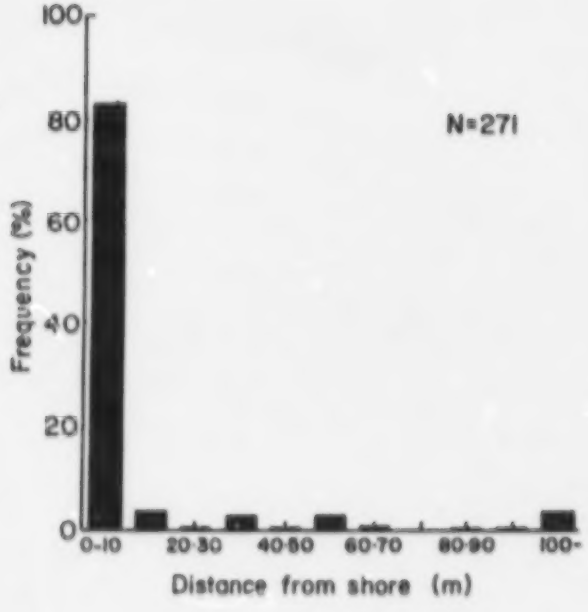


Fig. 5. Distance lake trout spawning sites are located from shore.

not seriously biased by the collection method (shoreline cruising), because of the results of the earlier work by McMurtry (1986). In a subset of this data set, he showed that sites located by tracking fish with attached ultrasonic transmitters were equally close to the shore as sites discovered visually.

We did not have complete information on the average width of spawning areas (the area where egg deposition occurs). Our present data simply records the distance of the closest edge of the spawning area to shore. In order to protect the full width of any sites within the target area, therefore, we suggest a distance from shore of <15 m. We propose a second rule:

RULE 2: DISTANCE FROM SHORE PRH = area of the lake <15 m from shore (including island shoreline)

McMurtry (1986) noted that only 1 of 221 confirmed spawning sites was within 20 m of a stream inlet. Although river spawning populations of lake trout did occur in some tributaries of the Great Lakes (Loftus 1958; OMNR unpubl. data), in inland lakes lake trout appear to avoid areas near stream inlets. This may be due to siltation in these areas. We propose a third rule:

RULE 3: DISTANCE FROM INLET PRH = area of the lake >20 m from any inlet

The presence of clean coarse substrate at lake trout spawning sites indicates that these are high energy sites, where silt and detritus are removed by wind-driven currents and waves. For our analysis, we hypothesized that some minimum fetch was needed to keep substrate clean. Only two sites in our data set (1%) had a fetch less than 0.5 km and only 10% had a fetch of less than 1.0 km (Fig. 6). The overall mean fetch was 2.96 km. We propose a fourth rule:

RULE 4: FETCH PRH = area of the lake with fetch >0.5 km

Martin (1957) recognized that lake trout spawning sites in a lake are often orientated in a way that exposes them to wind driven currents coming from a particular direction. In his study of Lake Louisa, orientation to the southwest was a striking feature of all sites (Fig. 7). If the orientation of sites on a lake is related to dominant wind patterns in an area, then spawning sites on lakes in close proximity to each other probably receive wind from the same direction. If this assumption is true then we can use the orientation of sites on sampled lakes to predict the likely location of spawning sites on nearby unsampled lakes.

To examine orientation of spawning sites, we combined data for lakes within an OMNR region. Only Algonquin, Eastern and Northeastern regions had large sample sizes (>50 sites). Northwestern Region is included, as well, but with its small sample size (4 lakes, 18 sites), the readers should be cautious about interpretation for that area.

We examined the potential directions from which wind-driven waves can reach a site. It is obvious that sites located on the edges of islands or points of shoreline are exposed to wind from many directions. However, many sites in a given region do exhibit common orientations. For example, in Algonquin Region approximately 50% of the sites were sheltered from easterly winds, while approximately 90% of the sites were exposed to wind from the west or southwest (Fig. 8).

Within each region, we measured the occurrence of sites with exposure to wind coming from a particular direction. We selected a minimal occurrence level of 80% as acceptable for the inclusion of compass orientation in classifying

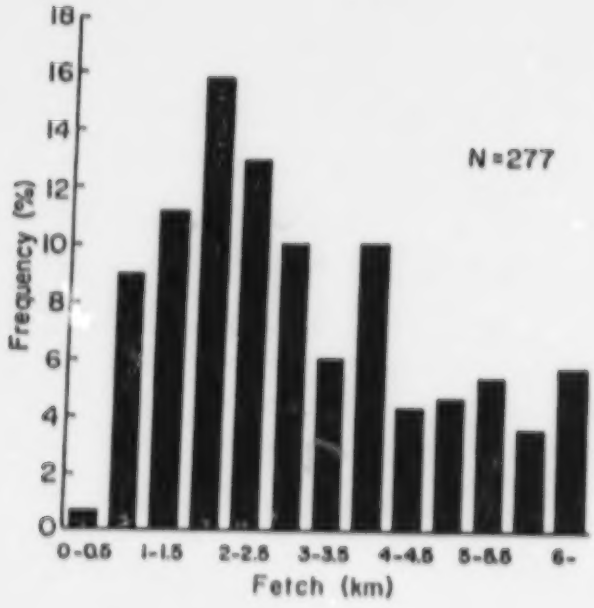


Fig. 6. Fetch at lake trout spawning sites.

Fig. 7. Orientation of known lake trout spawning sites in Lake Louisa, Algonquin Park, Ontario (Martin 1957).

potential reproductive habitat. In the four regions, the resulting high exposure directions were as follows: Algonquin Region, west (87.6%) and southwest (89.1%); Eastern Region, northwest (85.1%); Northwestern Region, west (88.8%); and Northeastern Region, north (87.3%) and northwest (85.5%) (Fig. 9). We propose a fifth rule:

> **RULE 5: ORIENTATION PRH = areas with direction of wind exposure similar to that of >80% of observed spawning sites in the region.**

Our survey of spawning sites generated a description of spawning substrate that matched that of Martin (1955). The substrate is generally very porous and appears to be free of heavy deposits of silt and detritus. Observers were usually only able to describe the substrate composition for the general area over which spawning occurred, rather than the specific areas where eggs were deposited. This general area contained a variety of particle sizes, with rubble (5-30 cm) - 50%, boulders (30 cm-1.0 m) - 23%, and gravel (0.1-5.0 cm) - 16% being the dominant size classes (Fig. 10). When eggs were actually observed, they usually occurred among rubble (Martin 1955; Liimatainen et al. 1987).

Clean open substrate appears to be an essential element of lake trout spawning habitat. The deep interstitial spaces in such substrate offer developing eggs and swim-up fry protection from predators. Such a hiding strategy makes sense if the substrate is free of large quantities of organic material; otherwise decomposition would result in anoxic conditions in the interstitial spaces during incubation. We propose a sixth rule:

> **RULE 6: SUBSTRATE SIZE PRH = area(s) of lake with clean coarse (5-30 cm) substrate**

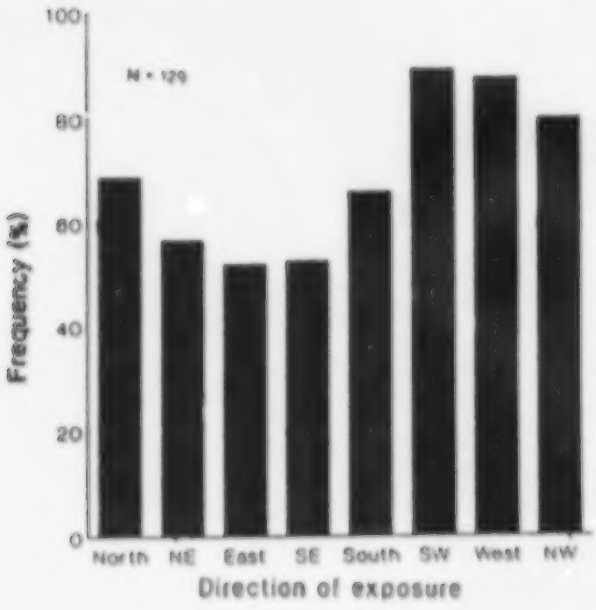


Fig. 8. Direction of wind exposure at 128 lake trout spawning sites in Algonquin Region lakes.

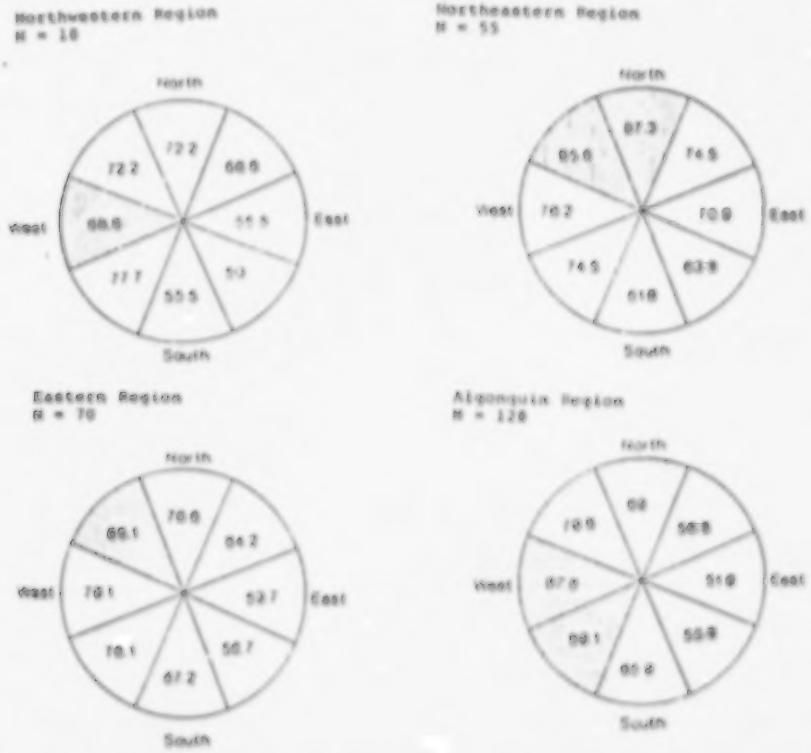


Fig. 9. Distribution of lake trout spawning by direction of potential wind exposure for four regions. High exposure wind directions (greater than 80% of sites receive wind from this direction) are shaded.

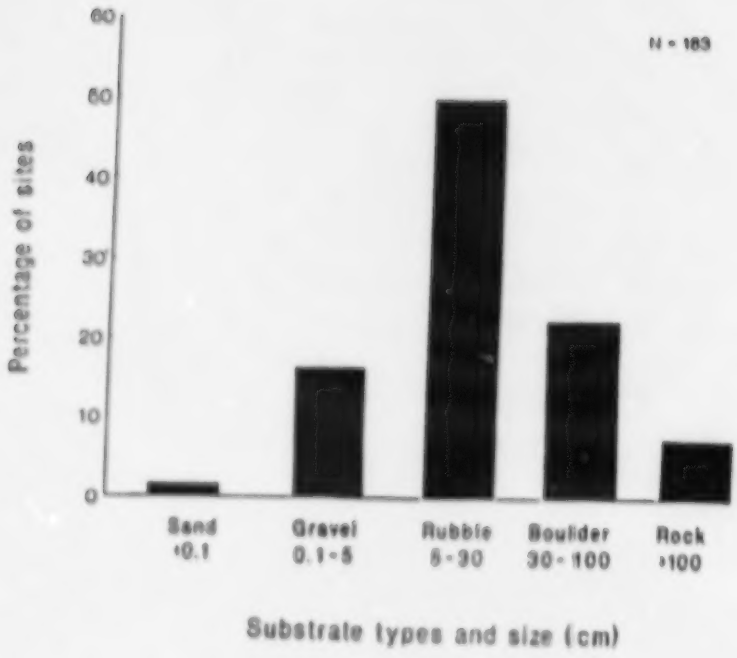


Fig. 10. Composition of substrate at lake trout spawning sites.

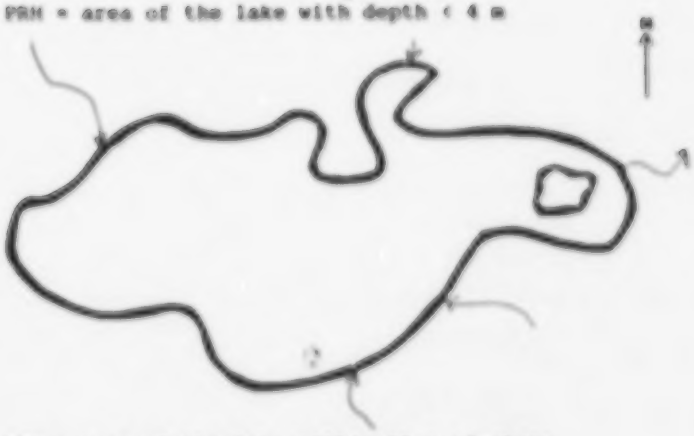
Our description of spawning site characteristics from this large data set generally confirms the suggestions made by Martin (1957). We are confident that the results of detailed studies on a small number of lakes can be used to provide useful management information for extrapolation to lakes outside our data set.

We weren't able to provide an easily applied rule to account for the observation that spawning sites are often near steep drop-offs. However, these sites are probably included by application of the existing rules. For example, steep shorelines are often the location of rubble beds, the result of rocks tumbling down from exposed rock faces.

Most of our rules for mapping spawning habitat can be applied quickly with very little background information. Rule 1 (depth) requires that a bathymetric map of the lake be available with depth contours to allow for the drawing of the 4 m line. Rules 2 (distance from shore), 3 (distance from inlets), and 4 (fetch) can be performed using a topographical map and a ruler. To use the orientation rule (#5), a manager needs a clear plastic template similar to one of those illustrated in Fig. 9. The template is lined up with the compass orientation of the map, and then depending on the region, only sites receiving wind from high exposure sectors are considered as likely spawning habitats. For Rule 6, the manager needs a map showing the composition of the substrate along the shoreline. Not all the rules need be applied to get a general idea of where spawning likely occurs. For example, the minimum fetch rule (#4), and the orientation rule (#5) will eliminate from further consideration any back bays and large areas of sheltered shorelines.

The procedure for applying these rules is illustrated in Fig. 11. Caution should be exercised when using this key. First, we have not yet tested these rules on lakes not in the data set. Second, we are dealing with probabilities for occurrence, therefore these rules will certainly miss some sites on some lakes. For instance, the orientation rule assumes that nearby lakes receive wind from the same direction. This assumption does not take into account the effects of local topography (hills, valleys, forest cover) and its effects on surface wind direction. Finally, this classification scheme is only for lake trout spawning habitat. It does not describe the habitat of other life stages of lake trout, nor can it be used for other species. Indeed the areas excluded by these rules (bays, sheltered areas) may be prime locations for other sport fish species such as walleye, bass (*Micropterus* spp.), and northern pike.

RULE 1: PRH = area of the lake with depth < 4 m



RULE 2: PRH = area of the lake within 15 m of shore

RULE 3: PRH = area of the lake greater than 20 m from any inlet

Fig. 11. Example of the use of a key to identify potential spawing sites of lake trout in Ontario lakes. In this example of a hypothetical Algonquin Region lake, the reproductive habitat for lake trout is the shaded area. The size of this area is reduced with the application of each successive rule.

RULE 4: PRM = area of the lake with fetch > 0.5 km

RULE 5: PRM = areas with direction of wind exposure similar to that of ≥ 80% of observed spawning sites in the region

RULE 6: PRM = area of lake with clean coarse (5.0 30.0 cm) substrate

Fig. 11. (continued)

MANAGEMENT STRATEGIES

Management strategies related to lake trout physiology and ecology are presented. Throughout this exercise, an underlying theme became increasingly clear: the need to preserve native lake trout stocks.

STRATEGY 1: IDENTIFY AND CONSERVE NATIVE LAKE TROUT STOCKS

Genetic differences among lake trout from different lakes and those spawning on different shoals in large lakes are associated with adaptation to local habitats. Introduced non-native stocks generally have lower fitness in their recipient habitat. If local stocks are lost, part of the genetic diversity and fitness of the species is lost. The loss in overall fitness can result in the loss of natural recruitment and fishing opportunities.

We recommend that managers identify the stock diversity and population status of all important lake trout stocks. Healthy wild stocks should be maintained by: protecting habitat (e.g. no net loss); protecting community integrity (e.g. no introductions of non-native fish; no non-native bait fish); and controlling harvest (e.g. maintain breeding population). If rehabilitation is necessary, consider habitat and community protection/rehabilitation and harvest control in conjunction with any stocking program.

STRATEGY 2: ENSURE THE GENETIC INTEGRITY OF NATIVE STOCKS WHERE STOCKING IS DEEMED NECESSARY FOR REHABILITATION

In general, transplanted lake trout raised in a hatchery have not performed as well as native stocks, in terms of survival and reproduction. Reproduction by non-native stocks often has not occurred or has been only partially successful. This poor performance is likely related to both genetic and environmental effects under hatchery conditions. Not only can artificial

selection result in a genetically inferior hatchery product but different environmental conditions in hatcheries (e.g. temperature, light) can permanently alter morphological, physiological and behavioral characteristics.

Fisheries managers can avert potential adverse hatchery effects related to genetics (selection) and the environment by: following established brood stock management guidelines; paying greater attention to the environmental history of brood stocks; collecting reproductive products annually; stocking early life stages; and closely matching hatchery environmental conditions to those in receiving waters.

For rehabilitation or reintroductions, we recommend that the selection of a stock should be in the following descending order of priority: same shoal; same lake; a sanctuary stock from a previously established genetic "refugium"; same watershed from a biotically and abiotically similar community; a hatchery stock originating from a habitat which closely matches receiving waters.

STRATEGY 3: DISCONTINUE SUPPLEMENTAL STOCKING IN LAKES WITH NATURALLY REPRODUCING LAKE TROUT STOCKS

Supplemental stocking can have a negative impact on wild stocks through: predation of planted yearlings on younger naturally reproduced lake trout; competition between hatchery and naturally reproduced yearlings; introgression; the physical displacement of native fish from spawning sites; and socioeconomic factors (planting fish may increase the exploitation rate on native wild stocks).

We recommend that the supplemental stocking of naturally reproducing lake trout lakes should be discontinued. Managers should opt for habitat and community protection/rehabilitation and harvest control as a first option. Client groups should be better educated about realistic resource expectations.

STRATEGY 4: PROVIDE ADDITIONAL FISHING OPPORTUNITIES FOR LAKE TROUT BY STOCKING THIS SPECIES IN LAKES WITH SUITABLE HABITAT BUT WHERE LAKE TROUT ARE NOT PRESENT

We recommend that lake trout should be introduced into lakes devoid of that species if such lakes have suitable environmental conditions for lake trout. This will provide additional fishing opportunities for lake trout. More importantly, this strategy will provide the incentive to protect these waters as lake trout habitat. Less stringent environmental protection may be enforced if such waters are managed for other fish species. The objective of these introductions is to establish self-sustaining, naturally reproducing populations.

STRATEGY 5. DISCONTINUE AND PREVENT THE INTRODUCTION OF FOOD ITEMS FOR LAKE TROUT

It is the quality, quantity and availability of prey type, together with fishing mortality that determines the potential growth patterns of a stock, and the observed size composition of a lake trout population. Populations which rely on fish for food are characterized by good growth and have the potential to reach trophy size. In the absence of pelagic forage fishes, particularly during the period of thermal stratification, lake trout are usually slower growing, early maturing and shorter lived.

Managers, faced with increasing demand for angling opportunities in food-limited environments, have tried to enhance growth by the introduction of exotic prey species. While there have been a few successes, in general, introductions, either intentional or accidental, have proved destructive to not only lake trout, but the entire fish community. We recommend that fisheries managers discontinue the practice of introducing food items to increase lake trout growth and prevent unintentional introductions of exotic food items into lake trout communities.

STRATEGY 6: MAINTAIN EXISTING LAKE TROUT HABITAT, REHABILITATE FORMER LAKE TROUT HABITAT WHERE FEASIBLE, AND CREATE LAKE TROUT HABITAT WHERE POSSIBLE

Under the Fisheries Act, "fish habitats" are defined as those parts of the environment "on which fish depend directly or indirectly, in order to carry out their life processes". The federal Department of Fisheries and Oceans (1986) described the net gain of fish habitat as the overall intent of its policy for the management of fish habitat. The goals of this policy are to: maintain current productive capacity of fish habitats, using no net loss as a guiding principle; rehabilitate the productive capacity of fish habitats in selected areas; and create and improve fish habitats in selected areas where production can be increased.

We recommend that managers use the plan review process and existing legislation to protect lake trout habitat from degradation. Local Ministry of Natural Resources managers must closely examine all development proposals for potential alteration, disruption or destruction of fish habitat. District management plans should target former lake trout lakes for rehabilitation where possible, e.g. nutrient input control, spawning shoal cleaning,

restocking. Finally, we should further investigate techniques to create and enhance lake trout habitat (e.g. spawning shoal creation).

STRATEGY 7: MAINTAIN EXISTING LAKE TROUT HABITAT AS A FIRST PRIORITY. TO PROTECT SELF-SUSTAINING LAKE TROUT POPULATIONS MAINTAIN GREATER THAN 20% OF THE TOTAL LAKE VOLUME AS OPTIMUM HABITAT AND 40% OF THE TOTAL LAKE VOLUME AS USEABLE HABITAT

OMOE and OMNR (1986) developed a model to predict the percentage loss in optimum habitat in a lake after a 100 kg increase in phosphorus supply. They proposed that shoreline development be discontinued on lake trout lakes that lose >50% of their optimum habitat; while restricted development be allowed to proceed on others. Inherent in this decision, is an assumption that some optimum habitat can be sacrificed without jeopardizing the lake trout fishery. Our investigations suggest that lake trout lakes with less than 20% optimum and 40% useable habitat are more sensitive to stress. We recommend that to protect self-sustaining lake trout populations, the optimum and useable habitat volumes exceed 20 and 40% of the total lake volumes.

STRATEGY 8: IDENTIFY AND PROTECT LAKE TROUT SPAWNING HABITAT

There are "unique" sites on a lake that are selected for spawning by lake trout. Lake trout spawning sites can be identified through shoreline cruises during the spawning run. In the absence of field data, we recommend that the key be used to identify likely spawning site locations.

Spawning sites must be protected from the detrimental effects of water drawdown and shoreline alterations. On lake trout lakes where water levels are controlled, we recommend that drawdowns be completed before spawning commences. Sites also need to be protected from substrate extraction,

infilling (beaches), and siltation (erosion) to maintain the deep well-oxygenated interstitial substrate pores; the microhabitat of wintering embryos.

ACKNOWLEDGEMENTS

The working group wishes to thank the many individuals in OMNR and OMOE who provided data and technical advice. We are also grateful to C.H. Olver and two anonymous reviewers for their comments.

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Appendix A: Summary of physical characteristics, optimum habitat, useable habitat and reproductive status for 151 lake trout lakes in Algonquin and Eastern regions, OMNR.

Lake	District	Surface area (ha)	Volume ($m^3 \times 10^6$)	Percentage optimum habitat	Percentage useable habitat	LT origin
Anstruther	52	625.3	80.00	45.2	55.1	N3
Art	54	126.3	9.60	0.0	2.0	N1
Ashby	66	266.0	30.84	18.5	44.0	N3
Ashden	66	138.0	13.69	16.4	24.6	N3
Aylen	51	2016.0	548.00	51.3	59.3	N1
Bailey	66	7.0	0.73	0.0	19.2	N5
Barber	66	173.0	22.11	44.6	57.4	N3
Barnard	66	39.0	7.35	21.9	56.5	N1
Beech	54	124.0	2.30	0.0	18.1	N5
Big Clear	64	187.4	24.27	44.5	57.9	N3
Big Chiman	66	32.0	6.57	7.8	15.4	I3
Big Salmon	64	148.1	22.90	34.0	50.0	N3
Big Trout	54	204.0	18.88	37.2	47.3	N1
Bighawk	57	365.2	65.96	56.1	63.3	N3
Birch	64	195.0	34.00	23.4	62.5	N3
Bitter	54	42.9	5.92	17.7	32.5	I2
Black	54	68.0	4.32	0.0	0.0	E
Boshkung	54	716.4	166.70	62.1	65.1	N3
Buck	52	36.2	3.32	35.3	46.4	N1
Buck (N.Basin)	64	264.0	27.78	0.0	25.1	N5
Buck (S)	64	491.0	60.90	11.8	51.0	N3
Camp	53	189.3		53.8	61.7	N1
Canning	54	244.1	340.08	0.0	0.0	N5
Canoe	64	291.0	66.69	44.6	68.7	N3
Canonto	61	224.0	14.77	0.0	19.0	E
Centre	52	144.1	9.76	0.1	0.0	E
Charleston	61	2917.2	433.10	47.9	66.0	N3
Clean	54	160.0	23.90	34.3	42.9	N1
Clinto	53	137.6	11.05	1.9	6.7	N3
Crow	66	442.0	89.75	21.2	54.2	N3
Crystal	66	50.0	4.69	38.2	55.2	N1
Crystal	54	483.2	54.14	3.9	10.8	N5
Deer	52	189.7	16.04	0.0	24.2	N3
Delano	51	29.1	1.70	0.0	0.0	N1
Delphia	54	26.4	2.67	12.9	26.4	N1
Desert	64	402.0	81.10	55.0	67.0	N3
Devil	64	1061.9	152.00	29.5	57.7	N3
Dickson	51	975.0	53.60	0.0	0.1	N1
Dicky	66	214.0	37.93	58.3	70.6	N3
Dog (N.E.Basin)	64	229.0	39.90	46.1	56.6	N5
Dotty	53	153.8	10.75	24.4	30.7	I2
Eagle	54	234.7	16.58	0.0	13.1	N5
Eagle	66	646.0	83.68	19.2	46.4	N3
Effingham	66	197.0	18.47	14.7	45.9	N3
Elsevir	66	14.0	1.52	5.9	17.8	I2

Appendix A (continued)

Lake	District	Surface area (ha)	Volume ($m^3 \times 10^6$)	Percentage optimum habitat	Percentage useable habitat	LT origin
Esson	54	239.8	26.59	11.6	52.6	N3
Eyre	54	65.6	5.19	12.9	31.2	N1
Fairy	53	711.5	158.25	58.3	69.0	N5
Farquhar	52	336.1	59.39	54.4	66.5	N3
Fishtail	52	246.9	44.18	55.8	61.3	N1
Glamour	54	194.8	19.77	0.0	5.6	N5
Gold	54	317.6	49.80	58.0	63.8	N3
Gooderham	54	87.0	5.94	0.0	0.0	E
Grace	52	226.4	34.73	55.3	65.2	N3
Grimsthorpe	66	94.0	7.23	5.8	37.6	N5
Gull	54	995.8	164.86	19.3	52.6	N1
Haliburton	54	1012.9	179.51	52.3	55.7	N3
Halls	54	543.2	153.30	65.0	67.6	N3
Havelock	54	196.3	20.03	23.9	36.4	I2
Hudson	52	73.7	8.22	13.0	30.3	N3
Hungry	66	255.0	10.54	0.0	25.5	I3
Indian	61	266.0	30.35	0.0	15.4	N5
Joe Perry	66	169.0	12.35	0.0	33.5	N3
Johnson	54	151.1	27.75	14.0	78.9	I3
Kabakus	54	113.6	7.65	0.0	13.8	I2
Kashagawigan	54	817.9	106.66	42.8	52.4	N3
Kashwakamak	66	1172.0	59.16	17.0	28.0	E
Kawagama	53	2821.0	599.15	53.3	56.7	N1
Kelly	54	98.6	11.58	25.5	65.0	I3
Kennisis	54	1417.4	322.03	52.8	66.2	N3
Kimball	53	212.5	48.66	65.0	67.5	N1
Kishkebus	66	85.0	11.43	15.8	57.3	N3
Knowlton	64	182.0	27.83	23.0	46.6	N3
Leviella	51	2402.0	346.00	41.1	48.0	N1
Lipsy	54	69.0	12.09	62.2	62.4	I2
Little Mackie	66	53.0	6.34	30.8	42.3	N5
Little Black	54	21.9	1.66	5.8	14.8	N1
Little Clear	64	55.0	7.78	29.3	35.7	I2
Little Green	66	29.0	4.49	20.3	35.6	N3
Little Hawk	57	346.3	108.61	69.5	69.8	N3
Little Kennisis	54	229.6	35.24	13.6	70.0	I3
Little Merrill	66	57.0	3.31	0.0	38.1	N5
Little Salmon	64	38.0	6.35	33.5	54.0	I2
Long	52	95.5	8.96	0.0	39.0	N1
Long	53	109.4	13.03	13.9	34.2	I3
Long Mallory	66	63.0	4.97	10.7	31.4	N5
Long Schooner	66	200.0	14.08	0.0	10.2	E
Loon	53	31.5	1.57	0.0	4.6	N3
Loucks	52	34.5	2.61	0.0	0.0	N5
Loughborough(W)	64	738.0	107.99	12.0	48.2	N5
Louisa	51	490.0	83.30	57.0	60.5	N1
Lower Beverly	41	767.0	65.68	0.0	0.0	E

Appendix A (continued)

Lake	District	Surface area (ha)	Volume ($m^3 \times 10^6$)	Percentage optimum habitat	Percentage useable habitat	LT origin
Lucky	66	100.0	11.82	14.0	29.1	R3
MacDonald	54	127.8	14.97	19.8	37.5	R1
Mackie	66	158.0	13.74	6.7	33.9	R3
Mair	66	49.0	7.07	21.1	29.7	I2
Marble	66	176.0	7.05	9.4	20.0	S
Marsden	54	230.2	8.76	0.0	9.3	R1
Mary	53	1066.3	263.44	57.1	62.9	R3
Masinaw	66	1592.0	686.91	78.9	85.9	R3
McCausland	66	36.0	4.07	18.4	35.6	I2
Miskwabi	54	263.8	52.20	63.0	66.9	I3
Mississeagaon	66	507.0	45.06	10.0	29.0	S
Monmouth	54	76.6	6.41	0.0	34.0	I2
Moose	54	289.7	40.33	50.1	62.5	R3
Moose	66	138.0	10.20	0.0	12.2	R5
Mountain	52	143.4	2.13	0.0	7.6	R3
North	54	83.1	12.93	57.1	64.8	I2
Nunikani	57	115.7	9.19	10.0	31.8	R5
Opeongo	51	5860.0	956.00	32.1	41.7	R1
Otter	61	603.0	78.15	0.0	4.3	R5
Otter (Cutter)	66	229.0	26.31	31.2	58.5	I3
Palmerston	66	563.0	115.90	53.1	62.2	R3
Peudash	52	756.8	89.61	49.4	58.5	R3
Peninsula	54	866.8	84.61	27.2	38.5	R3
Percy	54	605.7	77.10	8.9	64.6	I3
Picard	54	75.8	7.62	2.2	13.1	R5
Pusey	52	56.7	6.04	9.4	30.6	I2
Raven	57	560.7	46.35	30.3	38.8	R5
Rebecca	53	210.5	16.61	23.4	31.9	R5
Redhorse	61	302.0	30.62	0.0	47.7	R5
Redpine	57	383.9	41.08	36.6	42.4	R3
Redrock	51	293.0	18.20	32.6	39.2	R1
Reid	66	105.0	8.09	0.0	17.8	P*
Rideau	61		799.97	39.1	70.1	R3
Round Schooner	66	192.0	28.86	32.0	44.7	R3
Rustyshoe	54	30.0		0.0	0.0	S
Salmon	54	171.9	19.74	17.8	36.5	R3
Shabomeka	66	265.8	33.99	27.4	52.3	R3
Sherbut (West)	66	684.0	63.83	6.0	25.8	R3
Shaldon	54	52.9	4.86	0.0	41.8	I2
Sherborne	57	252.0	24.31	21.2	39.7	R3
Silent	52	118.3	7.60	0.0	20.5	R3
Silver	63	246.0	25.04	14.3	27.6	I2
Simpson	66	25.0	2.63	11.8	25.1	R5
Skeutamatta	66	742.0	54.61	0.0	24.0	S
Skeutamatta W.	66	456.0	29.53	0.0	47.0	S
Slipper	53	51.7	7.36	26.6	46.1	R1
Smoke	56	607.0	98.30	51.3	59.3	R3

Appendix A (continued)

Lake	District	Surface area (ha)	Volume ($m^3 \times 10^6$)	Percentage optimum habitat	Percentage useable habitat	LT origin
Smoke	51	407.0	98.30	51.3	59.3	M1
South Wildcat	54	96.7	20.22	51.2	62.0	I2
Spring	66	47.0	3.12	0.0	6.7	I2
St. Nora	57	263.9	41.93	93.6	98.1	M3
Thanet	66	112.0	8.76	4.0	18.0	M3
Timberwolf	51	167.0	11.70	0.0	0.0	M1
Trout (Len)	66	158.0	22.91	20.0	96.6	I3
Twelve Mile	54	336.8	40.87	8.7	34.6	M3
Upper Rideau	61	1363.0	115.73	0.0	0.0	S
Wanaley	68	571.0	126.30	96.0	65.0	M3
Waslemkoon	66	1968.0	168.70	27.1	31.0	I3
White Partridge	51	575.0	84.44	51.3	60.2	M1